77-12,740

HUNSICKER, James Philip, 1950-
MULTIPLE RETENTION DEFICITS IN RATS.

The University of Oklahoma, Ph.D., 1976
Psychology, experimental

Xerox University Microfilms, Ann Arbor, Michigan 48106

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

MULTIPLE RETENTION DEFICITS IN RATS

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

JAMES P. HUNSICKER

Norman, Oklahoma

1976

MULTIPLE RETENTION DEFICITS IN RATS

APPROVED BY

DISSERTATION COMMITTEE

ACKNOWLEDGEMENTS

I wish to express my sincere gratitude and appreciation to Dr. Roger Mellgren who took me under his wing and taught me to appreciate the external aspects of organisms. His standard and scope of excellence in research, teaching and friendship has provided a model to guide my development. I will be eternally indebted to him. I will also be eternally grateful to Dr. Larry Reid who sparked my interest in Psychology and who has remained my friend and advisor throughout the years. I would also like to thank Dr. Roger Fouts, Dr. N. Jack Kanak, Dr. Larry Toothaker and Dr. Michele Mondani for their continuous interest, care, and encouragement. A special thanks to Michele Steigleder for her companionship, encouragement and tea, and for giving me a swift kick anytime my feet began to drag. Thank you Marla Frick for typing this dissertation and assuming the role of my mother whenever I began to go astray.

I dedicate this dissertation to my father, Dr. A. L. Hunsicker, who is an open-minded and patient educator, counselor, seeker of knowledge and leader in every aspect of these words. He is the ultimate force and inspiration behind my development. Thank you for being there, dad.

TABLE OF CONTENTS

Page

Manuscript to be submitted for publication

INTRODUCTION. 1

GENERAL METHOD. 4

EXPERIMENT I 5

EXPERIMENT II. 9

EXPERIMENT III 10

EXPERIMENT IV. 14

GENERAL DISCUSSION. 19

REFERENCES. 21

TABLES. 24

FIGURES 26

APPENDICES. 30

APPENDIX A . . . . Background 30

APPENDIX B . . . . Statistical Tables . . 54

Abstract

In a series of experiments the multiple retention deficit phenomenon was studied with rats. In Experiment I, the number of passive avoidance acquisition trials was varied (1- and 5-trials). During passive avoidance testing which followed acquisition by 6, 12, 18, or 24 h, retention deficits at 6 and 18 h were observed for the 1-trial groups and not for the 5-trial groups. Therefore, the multiple retention deficit phenomenon appears to be restricted to limited training procedures. Experiment II was an exposure control replication of the first experiment. The 1- and 5-trial exposure groups did not demonstrate a performance deficit during the subsequent testing period. In Experiment III, the effects of an interpolated avoidance reduction procedure (flooding) administered at 0.25, 6, 12, 18, or 23.75 h after one-trial passive avoidance acquisition were examined during passive avoidance testing which followed acquisition by 24 h. Flooding was found to interact with retention performance to a greater extent when given 0.25, 12, and 23.75 h after acquisition. Finally, in Experiment IV, appetitive preexposure (sugared-milk in the shock compartment) was found to interact with (reduce) subsequent one-trial passive avoidance acquisition, tested 24 h after acquisition, more when administered 0.25, 9, 12, and 24 h prior to acquisition than when given 3, 6, 15, and 18 h prior to acquisition. Thus, the retention function for the appetitive event demonstrated multiple retention deficits similar to the deficits found after an aversive event. The results of Experiments I, III, and IV verify the multiple

retention deficit phenomenon reported previously by Holloway and Wansley (1973a, b). The results were discussed in the context of Holloway and Wansley's (1973b) state-dependent retrieval hypothesis of the multiple retention deficit phenomenon.

Introduction

Recently, Holloway and Wansley (1973a) found multiple retention deficits in rats at certain intervals after one-trial passive avoidance training. They reported higher retention performance (i.e., lower step-through latencies) at 15 min or multiples of 12 h after training than at 6 h after training or multiples of 12 h from the 6 h interval. The retention deficits appeared to wane at the longer intervals (i.e., 66 h) while the peaks remained the same out to the 72 h interval. Later, Holloway and Wansley (1973b) replicated the multiple retention deficit phenomenon with the same one-trial passive avoidance procedure and during the relearning phase of a multitrial, one-way active avoidance procedure. Wansley and Holloway (1975) extended the generality of the phenomenon to retention of an appetitively motivated response by demonstrating it during the relearnig phase of an one-trial appetitive maze training procedure.

Holloway and Wansley (1973b) suggested that the initial decrement in the multiple retention deficit phenomenon may be related to the "Kamin effect" (Kamin, 1957) which is empirically defined as a deficit in performance at some intermediate interval (1-8 h) following training (see Brush, 1971). This suggestion is based on the observation that the majority of research supporting the Kamin effect has employed close approximations of Kamin's (1957) original posttraining intervals (i.e., 0.5, 1, 6, and 24 h and 19 days). These intervals do not represent a systematic sampling of intervals within a 24 h period and therefore, may produce an incomplete pattern of the temporal parameter of retention performance. The only exception to this observation is a study by Caul, Barrett, Thune, and Osborne (1974) which assessed Y-maze avoidance in rats after Holloway and Wansley's training-testing intervals (TTIs), (i.e., 0.25, 1, 6, 12, 18, 24, and 30 h). Instead of multiphasic retention deficits following training, they observed a single retention deficit which was at the 1 hour interval (Kamin effect). However, there was a confound between deprivation level and the TTIs which could partially account for the differences in results. It will be assumed here that the findings and explanations associated with the Kamin effect at least have partial applicability to the multiple retention deficit phenomenon.

Most explanations of the Kamin effect have assumed that the testing performance decrement is caused by fluctuations in processes related to footshock. Denny and Ditchman (1962) proposed that fear incubates over time and at its maximum interfers with responding. Pinel and Cooper (1966) suggested an incubation of immobility hypothesis in which aversive training produces a decrease in reactivity, reaching a minimum at intermediate intervals, then an increase back to normal levels. Brush, Myer, and Palmer (1968) postulated a "parasympathetic over-reaction" following fear conditioning which interfers with normal posttraining avoidance responding. Klein and Spear (1970) proposed that shock or any stressor induced changes in ACTH levels after training produce a state-dependent retrieval deficit similar to that found in drug research (Overton, 1964). Research which has demonstrated the Kamin effect with appetitively motivated responses (Caul et al., 1974; Tribhowan, Rucker, and McDiarmid, 1971) calls into question the dependency on shock, per se, in explaining the Kamin effect, and may indicate that the effect reflects a relatively general phenomenon.

Holloway and Wansley (1973b) utilized the general tenets of Klein and Spear's (1970) state-dependent retrieval explanation of the Kamin effect by postulating that some undetermined constellation of periodically (12 h) fluctuating internal events define the state of the organism at the time of training, and shifts from this training state influence retention performance via the decreased availability of relevant cues. Holloway (1976) reported evidence which indicated that the relevant state changes are probably endogenous rather than some task-induced rhythmic process(es). He found that interpolated noncontingent shock in the same or a different apparatus only interacted with active avoidance retention performance, which was tested 24 hours after training, when given at 0.25, 12, or 23.75 hours posttraining, with no effect when given 6 or 18 hours posttraining. According to Holloway's reasoning, a shock-induced state change should be reset by interpolated shock and therefore, always affect retention performance while an endogenous rhythm is only available to be affected during training or 12 hour multiples of training. Holloway and Sturgis (1976) designed an experiment in which the critical retention interval was different than the interval between exposure to the training procedure and testing. They only found the multiple retention deficits for the critical retention intervals. This finding also supported the endogenous nature of the state change.

The purpose of the present set of experiments was to test the generality of the multiple retention deficit phenomenon. Experiment I examined the effects of the degree of original learning on the phenomenon by administering 1- or 5-trials of passive avoidance acquisition training. Experiment II controlled for differences in apparatus exposure during acquisition in Experiment I and provided a general control for the effects of fluctuating processes unrelated to training (e.g., activity) on testing performance. Experiment III examined the effectiveness of an interpolated procedure in reducing avoidance performance when administered at various intervals between passive avoidance acquisition and testing. Finally, Experiment IV was an attempt to extend the phenomenon to the retention of an appetitively motivated response without the deprivation confound present in Wansley and Holloway's (1975) appetitive procedure.

General Method

Subjects. All subjects were male albino rats of the Sprague-Dawley strain between 300 and 400 days old at the onset of the experiments. Subjects were individually caged in a temperature and humidity controlled environment with continuous illumination and ad lib. food and water.

Apparatus. The only apparatus used in this series of experiments was a wooden box measuring 90 cm long, 14 cm wide, and 30 cm deep. The apparatus was divided in two equal sized compartments (one black, one white) by a clear Plexiglas guillotine door. The grid floor consisted of aluminum tubes 13 mm in diameter, spaced 4 cm center-to-center. The entire apparatus was covered by a hinged hardware cloth top. A Grason-Stadler shocker (Model 700) was used to deliver a scrambled shock of 0.8 mA.

Procedure. Beginning 3 days prior to any experimental manipulations, all subjects were handled for approximately 3 minutes per day.

Passive avoidance acquisition consisted of placing the subject in the safe compartment (white side) facing the wall opposite the door to the shock compartment (black side). When the subject oriented toward the shock compartment, the door was raised. When the subject entered the shock compartment (defined as the back paw reaching the second bar in the shock compartment) the door was lowered and the subject received a 5-second 0.8 mA shock. The subject was then returned to its home cage. Acquisition training consisted of one trial. Before each subject was placed in the apparatus, fresh paper was placed below the grid floor and the floor and sides were washed with sponge and water.

The procedure for passive avoidance testing was identical to the training procedure with the exception of shock. The testing measure was the subject's latency to enter the shock compartment (step-through latency). Any subject failing to enter the shock compartment within 900 sec was removed from the apparatus and a step-through latency of 900 sec was recorded.

Experiment I

The Kamin effect has typically been found when the learning is incomplete (e.g., incompletely learned shuttlebox avoidance) or brief (e.g., one-trial passive avoidance). Anderson, Johnson, Schwendiman, and Dunford (1966) found the most pronounced single retention deficit following a 1-trial shuttlebox avoidance criterion and either less pronounced or no deficit following a 2 or 3 trial avoidance criterion. Klein and Spear (1970) only observed the Kamin effect when original one-way active avoidance training did not surpass a criterion of 10 consecutive avoidance trials.

The assumed relationship between the Kamin effect and the multiple retention deficit phenomenon (Holloway & Wansley, 1973a) suggests that the latter may also be characteristic of incomplete or brief original training. Accordingly, the multiple retention deficit phenomenon is based on research which has used brief learning periods (e.g., one-trial passive avoidance; one-trial appetitive maze training). The purpose of the present experiment was to examine the effects of degree of original training on the phenomenon by administering 1- or 5-trials of passive avoidance acquisition training and then, testing passive avoidance after 6, 12, 18, or 24 h. The acquisition was administered at one of two times of day to permit assessment of circadian variables on retention performance at the various acquisition-testing interval conditions.

Method

Procedure. Sixty-four rats were randomly assigned to 1 of 16 independent groups (n=4 per group). The groups were defined by 2 acquisition times (0600-0900 h or 1200-1500 h), 2 degrees of training (1- or 5-trials acquisition), and 4 acquisition-testing intervals (6 h, 12 h, 18 h, or 24 h) factorially combined.

All subjects received the one-trial passive avoidance acquisition procedure which was described above, with half of the subjects receiving 4 additional training trials. The only procedural differences in the additional trials were that the subjects were placed directly into the shock compartment of the apparatus at the onset of the trial, and shock followed placement by 5 sec. During the four 60 sec intertrial intervals, the 5-trial subjects were placed in a holding cage. In order to equate the duration of training and the amount of subject handling between the 1- and 5-trial groups, the 1-trial subjects were also placed in a holding cage after their acquisition trial, and then every 60 sec for 4 min they were taken out and handled for about 20 sec (approximate duration of each acquisition trial). Then, either 6, 12, 18, or 24 h following acquisition, the subjects were tested for passive avoidance under the procedure previously described.

Results

A 2 x 2 x 4 factorial analysis of variance on testing step-through latencies showed a significant difference between the 2 degree of training treatments, $F(1,48)=5.69$, $p < .01$, and between the 4 acquisition-testing interval treatments, $F(3,48)=2.75$, $p < .01$. The 2 acquisition time treatments and all interactions did not reach significance. Figure 1 shows the mean testing step-through latencies for the 2 degrees of training groups (1- and 5-trial groups) at the 4 acquisition-testing interval conditions (6, 12, 18, and 24 h) collapsed

Insert Figure 1 about here

across the acquisition time variable. The retention curve for the 1-trial groups is phasic with performance being lower at 6 and 18 h after acquisition than at 12 and 24 h posttraining; while the retention curve for the 5-trial groups is roughly linear across the 4 posttraining intervals. Tukey's pairwise comparisons confirmed these effects. The comparisons for the 1-trial groups showed that the 6 and 18 h interval treatments were not significantly different from each other but were significantly different from the 12 ($t(4,40)=2.50$, $p < .06$ and $t(4,40)=2.68$, $p < .05$, respectively) and 24 h interval treatments ($t(4,40)=2.48$, $p < .06$ and $t(4,40)=2.80$, $p < .05$, respectively) which were also not significantly different from each other. There were no significant comparisons for the 5-trial treatments across the acquisition-testing intervals.

Discussion

The results of the 1-trial groups were characteristic of Holloway and Wansley's (1973a) multiple retention deficit findings, and thus, provides a replication (the first?) of the phenomenon outside of Holloway's laboratory. The lack of any retention performance deficits with the 5-trial groups indicates that the multiple retention deficit phenomenon may be confined to brief or limited training procedures. Similar extended training procedures with active avoidance have been shown to alter or eliminate the deficit in retention performance associated with intervals used in the "Kamin effect studies" (Anderson et al., 1966 and Klein & Spear, 1970). This similarity in results supports Holloway and Wansley's (1973a) suggestion that the initial decrement in the multiple retention deficit phenomenon may be related to, or synonymous with the Kamin effect.

Surprisingly, the 5-trial groups were not different from the 12 and 24 h interval groups of the 1-trial treatment in testing performance. This indicates that there is an asymptote in the degree of shock produced facilitation of passive avoidance under the present conditions. The absence of retention performance deficits for the 5-trial groups may be a result of this asymptotic strength concealing possible performance differences between groups.

Experiment II

The previous experiment did not control the amount of apparatus exposure between the 1- and 5-trial groups. Therefore, the present experiment assessed the effects of different amounts of exposure to the apparatus on testing performance. Since the testing performance differences associated with the multiphasic retention function occur in a 12 h post-training cycle, this experiment only utilized 6 and 12 h training-testing intervals (TTIs) to conserve subjects.

Method

Procedure. Thirty-two rats were randomly assigned to 1 of 8 independent groups (*n*=4 per group) which were defined by 2 training times (same as Experiment I), 2 degrees of apparatus exposure (1- or 5-exposure trials), and 2 TTIs (6 h or 12 h) factorially combined.

The training procedure was the same as Experiment I, except there was no shock. The subjects were exposed to the "shock" compartment during the 1- or 5-training trials. Testing followed training by 6 or 12 h and was identical to Experiment I.

Results

The mean testing step-through latencies for the 1-trial groups at the 6 h (6.6 sec) and 12 h (6.0 sec) TTIs were similar, but faster than the latencies for the 5-trial groups at the 6 h (13.6 sec) and 12 h (11.0 sec) TTIs which were also similar. An analysis of variance demonstrated that the degree of exposure variable was the only significant effect, $F(1,24)=10.1$, $p < .01$.

Discussion

Although the degree of apparatus exposure affects testing performance, it does so in a uniform manner for the two TTI conditions. Therefore, the different patterns of retention performance for the 1- and 5-trial groups in Experiment I could not have been produced by differences in exposure to the apparatus between the two groups.

The 1-trial exposure groups provide a general control for the one-trial passive avoidance procedure. The similarity of results at the two TTI conditions indicates that the multiple retention deficit phenomenon is due to fluctuations in training retention or fear, but not to fluctuations in process(es) which remain independent of training (e.g., activity).

Experiment III

Holloway (1976) administered interpolated noncontingent shock to rats at various intervals after active avoidance training, and tested for avoidance retention either 24 or 30 hours after training. In the 24 hour interval groups, he found that the interpolated shock interacted with retention performance (impaired it) when delivered 0.25, 12, or 23.75 hours after training, but had no effect on retention performance when given 6 or 18 hours after training. According to Holloway the results suggested that an endogenous rhythmic process(es) underlying state-dependent retrieval were not present to be affected by shock or anything at the 6 and 18 h TTIs, but were at the 0.25, 12, and 24 h TTIs. The reason for the 0.25, 12, and 24 h interpolated shocks impairing testing performance was not specified by Holloway, but was probably due to the extremely disruptive effects of noncontingent shock.

A procedure termed "flooding" has been shown to be extremely effective in facilitating the extinction of avoidance responding (Baum, 1966; Page & Hall, 1953). In this procedure the subject is placed in the feared situation for some period of time, usually 5 to 10 min, and prevented from making the avoidance response. In the case of passive avoidance, flooding would consist of placing the subject in the shock compartment for a period of time.

The purpose of the present experiment was to extend Holloway's (1976) experiment using a passive avoidance procedure with flooding rather than shock as the interpolated task. According to Holloway's results, flooding should be effective in reducing passive avoidance, which is tested after a 24 hour acquisition-testing interval, when administered at 0.25, 12, and 23.75 h after training, and have no effect when given 6 and 18 h after training.

Method

Procedure. Fifty rats were randomly assigned to 1 of 5 independent groups (n=10 per group). The groups were defined by 5 acquisition-flooding intervals, which were 0.25, 6, 12, 18, and 23.75 h.

The subjects were administered the one-trial passive avoidance acquisition and testing procedures previously described. The acquisition-testing interval was 24 h across the 5 groups. After their particular acquisition-flooding interval, the subjects received interpolated flooding. During flooding the subject was placed into the shock compartment and confined for 5 min.

Results

An analysis of variance on the testing step-through latencies yielded a significant difference between the 5 groups, $F(4,39)=4.76$, $p < .01$. Figure 2 depicts the mean testing step-through latencies

---

Insert Figure 2 about here

---

for the 5 acquisition-flooding groups. The curve is phasic with passive avoidance responding being lower in the 6 and 18 h treatments than the 0.25, 12, and 23.75 h treatments. Tukey's pairwise comparisons confirmed these effects, df=4,39 throughout (Table 1).

Insert Table 1 about here

Discussion

The results demonstrate that flooding reduces avoidance responding to a greater extent when given 0.25, 12, and 23.75 h after acquisition than when given 6 and 18 h after acquisition. Thus, the interpolated procedure interacted with retention performance reliably more at the posttraining times were superior retention performance has been reported by Holloway and Wansley (1973a).

This finding is similar to Holloway's (1976) results with interpolated shock and a 24 h TTI, with one important difference. Holloway found that the interpolated shock only interacted with retention performance when given 0.25, 12, and 24 h posttraining, and had no effect when given 6 and 18 h posttraining. A comparison of the retention performance in this experiment (Figure 2) with the retention performance of the 1-trial groups of Experiment I (Figure 1) reveals that the present performance was uniformly lower. This indicates that flooding affected (reduced) retention performance in all interval groups although the 6 and 18 h groups were affected less than the other groups. There are other differences (e.g., rats, time, etc.) between the two experiments which could account for the differences in testing performance. Therefore, Holloway's (1976) assumption that the endogenous rhythmic processes underlying his state-dependent retrieval mechanism (Holloway & Wansley, 1973b) is absent at poor retention intervals (e.g., 6 and 18 hours) would have to be modified to account for the present results. It would have to be assumed that the process(es) is less salient at the poor retention intervals. The most obvious reason for the differences in Holloway's and the present results is differences in interpolated events (i. e., shock vs exposure), although it could be due to other differences (e.g., training tasks, duration of interpolated exposure, light-dark cycle differences, etc).

A second interpretation of the results is that the interpolated procedure directly produced or became associated with the rhythmic fluctuations which are observed during testing. Therefore, the critical interval is the flooding-testing interval which yields the same intervals for the high and low levels of testing performance. The multiple performance deficits during testing are caused by fluctuations in the retention of the flooding exposure. The main criticism of this interpretation is that there is no evidence to show that mere exposure to a situation leads to subsequent avoidance of the situation. Since the subjects passivly avoid the shock compartment during testing in this experiment, the first interpretation seems more tenable. Under either explanation this procedure extends the generality of the multiple retention deficit phenomenon.

Experiment IV

Attempts to determine the retention function following appetitive training have produced conflicting results. Some investigators have found no retention deficits in the 24 h following training (Gabriel, 1968; Hablitz & Braud, 1972); others have reported a single retention deficit (Caul, Barrett, Thune, & Osborne, 1974; Tribhowan, Rucker, & McDiarmid, 1971). Unfortunately, none of these studies include a systematic range of TTIs during the 24 h following training as in Holloway and Wansley's (1973a, b) aversive conditioning experiments. In a recent experiment, however, Wansley and Holloway (1975) varied the TTI during the 24 h following training, and obtained a phasic retention function similar to that found in their aversive pradigms (Holloway & Wansley, 1973 a,b). They deprived rats of water for 24 h prior to one-trial appetitive maze training in which 5 min access to water was the reinforcer and tested for retention at intervals of 0.25, 1, 6, 12, 18, and 24 h. Retention at 0.25, 1, 12, and 24 h was greater than at 6 and 18 h.

Testing for appetitive retention across different time intervals poses two problems. First, the retention test must be sensitive enough to pick up differences when exposure to the appetitive event is brief, since either lengthy exposure or multiple trials make it difficult to pinpoint a specific time of occurrence of the appetitive event. Furthermore, Experiment I demonstrated that the multiple retention deficits only occurred after the lesser degree of two degrees of avoidance training. Second, motivational factors (deprivation time) must be controlled across the various intervals to prevent an interaction with possible retention fluctuations. Wansley and Holloway (1975) resolved the first problem but possibly not the second. They allowed all groups to have 10 min access to water 1 h prior to training, and 1 h prior to testing gave another 10 min access to water for all groups except those tested at 0.25, and 1 h. This procedure was designed to equate the degree of deprivation across groups, although the possibility of differing deprivation levels exists because the rats in the various groups were deprived to differing degrees at the time of the 10 min free access period, in addition to the obvious problems for the 0.25 and 1 h conditions. The present experiment attempted to overcome these two problems by employing a different procedure to study the appetitive retention function.

Rats were given access to a preferred solution, milk with sugar added, in the shock compartment of a passive avoidance apparatus. Following one of 8 intervals, the subjects received on one-trial passive avoidance acquisition and 24 h later were tested for the degree of avoidance. Using the same procedure, but only a 6 min interval between preexposure and passive avoidance acquisition training, Mellgren, Hunsicker, and Dyck (1975) found that the appetitive preexposure significantly reduced the amount of passive avoidance behavior when compared to rats either not preexposed or rats given exploratory preexposure to the shock compartment. The interval between preexposure and passive avoidance acquisition and between preexposure and testing were the only conditions which varied between groups in the present experiment. Thus any differences between groups must be a function of differential retention of the appetitive preexposure either on the acquisition training trial or the testing trial. Either process would reflect the retention function for an appetitive event. Good retention of the appetitive preexposure should result in a short step-through latency during testing for passive avoidance, and poor preexposure retention should result in a long step-through latency during testing. The influence of circadian variables on retention was evaluated by administering preexposure at 1 of 2 time periods spaced 6 h apart. This procedure is sensitive, and since the appetitive preexposure consists of the presentation of a substance which does not require deprivation, motivational factors should not confound the preexposure retention function.

Method

Apparatus. The same apparatus as previously described was used here with one slight modification. During preexposure, a sugared-milk solution was placed in a jar lid, 3 cm in diameter, and attached to the rear wall of the black compartment. The sugared-milk solution consisted of table sugar and homogenized milk which was combined to yield a solution containing approximately 30 per cent sugar by weight.

Procedure. The rats were randomly assigned to 1 of 8 independent groups. The 8 groups were designated by their preexposure-passive avoidance acquisition intervals (PPI), which were 0.25, 3, 6, 9, 12, 15, 18, and 24 h. Five subjects in each PPI were preexposed at one time (0800-1100 h), while the remaining 4 subjects per treatment were preexposed 6 h later (1400-1700 h). Thus, the design of this experiment was a 2 (Preexposure time) x 8 (PPI) factorial.

During preexposure, each subject was placed in the white compartment of the apparatus and permitted access to the black compartment (shock side) where approximately 20 cc of sugared-milk was located. After entering the black side, the guillotine door was lowered and the subject was allowed 5 min access to the sugared-milk solution before being returned to its home cage.

The subjects were administered the one-trial passive avoidance acquisition and testing procedures previously described. The acquisition-testing interval was 24 h across the 8 groups. Training step-through latencies as well as testing step-through latencies were recorded.

Results

A 2 x 8 factorial analysis of variance on the testing step-through latencies yielded a reliable difference for the PPI main effect, $F(7,56)=7.35$, $p < .01$, but nonreliable differences between the 2 preexposure periods and PPI x preexposure period interaction. Figure 3 shows the mean testing step-through latencies for the 8 PPI treatments collapsed across the 2 preexposure periods. The retention curve is

----
Insert Figure 3 about here
----

phasic (retention of the appetitive preexposure is inversely related to step-through latency) with performance being lower in the 3, 6, 15, and 18 h treatments than the 0.25, 9, 12, and 24 h treatments. Tukey's individual pairwise comparisons confirmed these effects except that the 6 h PPI was only significantly different from the 9 and 24 h PPIs (See Table 2).

Insert Table 2 about here

The analysis of the training step-through latency produced nonreliable differences for both main effects and the interaction. The lack of reliable differences on this measure was probably due to a kind of ceiling effect, since all subjects entered the shock compartment at the start of passive avoidance acquisition in under 3 sec.

Discussion

The results of this experiment demonstrate that under the present conditions the retention function associated with an appetitive event is phasic. The symmetry of the 6 and 15 h groups on decline and incline, respectively indicates that whatever underlying process(es) is occurring has a symmetrical function not only at best and poorest retention intervals but also at intermediate retention levels. Since the time of preexposure variable did not yield reliable differences for any of the dependent variables, time-of-day variables can not account for the multiple retention deficits.

The present retention pattern is very similar to the multiple retention deficit phenomenon observed after avoidance responding by Holloway and Wansley (1973a, b) and after an appetitive task by Wansley and Holloway (1975). Ignoring the results of the 3, 9, and 15 h intervals in the present study, which were not included in Wansley and Holloway's study, the pattern of these two appetitive retention functions is very similar. Since deprivation was not manipulated in the present study, it is unlikely that the deprivation confound discussed earlier distorted the retention pattern present in the Wansley and Holloway study. The results of another study (Tribhowan, Rucker, & McDiarmid, 1971) which demonstrated poorer retention of an appetitive task at a 4 h interval than at 0.25, 8, or 24 h intervals also agree with the present findings. This deficit at the 4 h interval roughly corresponds to the deficit found at the 3 h interval when compared to the 0.25, 9, and 24 h intervals in the present experiment.

Since the multiple retention deficits associated with an appetitive event are similar to those found with an aversive event, the process(es) which underlies the fluctuations may be the same. This implies a general underlying process(es) which is not directly due to either the aversive or appetitive nature of the task. Holloway and Wansley's (1973b) state-dependent retrieval explanation satisfies this condition.

General Discussion

The present set of experiments verifies the multiple retention deficit phenomenon which was previously observed only in the Holloway Laboratory. Holloway and Wansley (1973b) proposed a state-dependent retrieval hypothesis of the phenomenon. According to this hypothesis the internal state of the organism during the training experience becomes an essential part of the conditioning and shifts away from that state influence retention performance via the decreased availability of relevant cues. Holloway and Wansley hypothesized that some undetermined pre-training endogenous rhythmic process(es) defined the state of the organism at the occasion of training and therefore, produced the multiphasic retention function. The endogenous rhythmic process(es) was assumed to be absent at those times when retention was poor (e.g., 6 and 18 h intervals).

Holloway and Wansley's state-dependent explanation of the phenomenon fits the present findings. This explanation is based on the saliency and relevancy of the organism's internal state during training. An extended training procedure, like the 5-trial acquisition treatment of Experiment I, would allow apparatus related stimuli (e.g., dark compartment) to have greater control over responding or the absence of responding.

The state-dependent retrieval hypothesis would also predict the observed interaction between flooding and training retention in Experiment III. Holloway's (1976) assumption of the absence of the rhythmic process(es) at intervals where retention was poor would have to be modified to state that the processes are less salient at those retention intervals. This model can account for the multiple retention deficits following either an aversive or appetitive training procedure.

References

Anderson, A. C., Johnson, L., Schwendiman, G., & Dunford, G. Retention of an incompletely learned avoidance response: Some problems with replication. Psychonomic Science, 1966, 6, 23-24.

Baum, M. Rapid extinction of an avoidance response following a period of response prevention in the avoidance apparatus. Psychological Reports, 1966, 18, 59-64.

Brush, F. R. Retention of aversively motivated behavior. In F. R. Brush (Ed.) Aversive learning and conditioning. New York: Academic Press, 1971.

Brush, F. R., Myer, J. S., & Palmer, M. E. Joint effects of inter-trial and intersession interval upon avoidance learning. Psychological Reports, 1964, 14, 31-37.

Caul, W. F., Barrett, R. J., Thune, G. E., & Osborne, G. L. Avoidance decrement as a function of training-testing interval: single cycle or multiphasic? Behavioral Biology, 1974, 11, 409-414.

Denny, M. R., & Ditchman, R. E. The locus of maximal "Kamin effect" in rats. Journal of Comparative and Physiological Psychology, 1962, 55, 1069-1070.

Gabriel, M. Effects of intersession delay and training level on avoidance extinction and intertrial behavior. Journal of Comparative and Physiological Psychology, 1968, 66, 412-416.

Holloway, F. A. Non-monotonic temporal gradients reflecting susceptibility of learned responses to interference. Submitted for publication, 1976.

Holloway, F. A., & Sturgis, R. D. Periodic decrements in retrieval of memory of non-reinforcement reflected in resistance to extinction. Submitted for publication, 1976.

Holloway, F. A., & Wansley, R. A. Multiphasic retention deficits at periodic intervals after passive avoidance learning. Science, 1973, 180, 208-210. (a)

Holloway, F. A., & Wansley, R. A. Multiple retention deficits at periodic intervals after active and passive avoidance learning. Behavioral Biology, 1973, 2, 1-14. (b)

Kamin, L. J. Retention of an incompletely learned avoidance response. Journal of Comparative and Physiological Psychology, 1957, 50, 457-460.

Klein, S. B., & Spear, N. E. Forgetting by the rat after intermediate intervals ("Kamin Effect") as retrieval failure. Journal of Comparative and Physiological Psychology, 1970, 71, 165-170.

Mellgren, R. L., Hunsicker, J. P., & Dyck, D. G. Conditions of preexposure and passive avoidance behavior. Animal Learning and Behavior, 1975, 3, 147-154.

Overton, D. A. State-dependent or "dissociated" learning produced with pentobarbital. Journal of Comparative and Physiological Psychology, 1964, 57, 3-12.

Page, H. A., & Hall, J. F. Experimental extinction as a function of the prevention of a response. Journal of Comparative and Physiological Psychology, 1953, 46, 33-34.

Pinel, J. P. J., & Cooper, R. M. Demonstration of the Kamin effect after one-trial avoidance learning. Psychonomic Science, 1966, 4, 17-18.

Tribhowan, T., Rucker, W. B., & McDiarmid, C. G. Demonstration of the Kamin like effect after appetitive training. Psychonomic Science, 1971, 23, 41-42.

Wansley, R. A., & Holloway, F. A. Multiple retention deficits following one-trial appetitive training. Behavioral Biology, 1975, 14, 135-149.

TABLE 1

Tukey's Pairwise Comparisons

	Testing-IEL (Sec)				
	.25 h 34.5	6 h 77.2	12 h 27.0	18 h 78.9	24 h 26.5
34.5		42.7*	7.5	44.4	8.0
77.2			50.2**	1.7	50.7**
27.0				51.9**	0.5
78.9					52.4**
26.5					

* $p < .05$

** $p < .01$

TABLE 2

Tukey's Pairwise Comparisons

	Testing-IEL (min)							
	.25hr 6.0	3hr 11.4	6hr 9.7	9hr 5.8	12hr 6.1	15hr 9.9	18hr 11.4	24hr 5.5
6.0		5.4**	3.7	0.2	0.1	3.9*	5.4**	0.5
11.4			1.7	5.6**	5.3**	1.5	0.0	5.9**
9.7				3.9*	3.6	0.2	1.7	4.2*
5.8					0.3	4.1*	5.6**	0.3
6.1						3.8	5.3**	0.6
9.9							1.5	4.4*
11.4								5.9**
5.5								

* $p < .05$

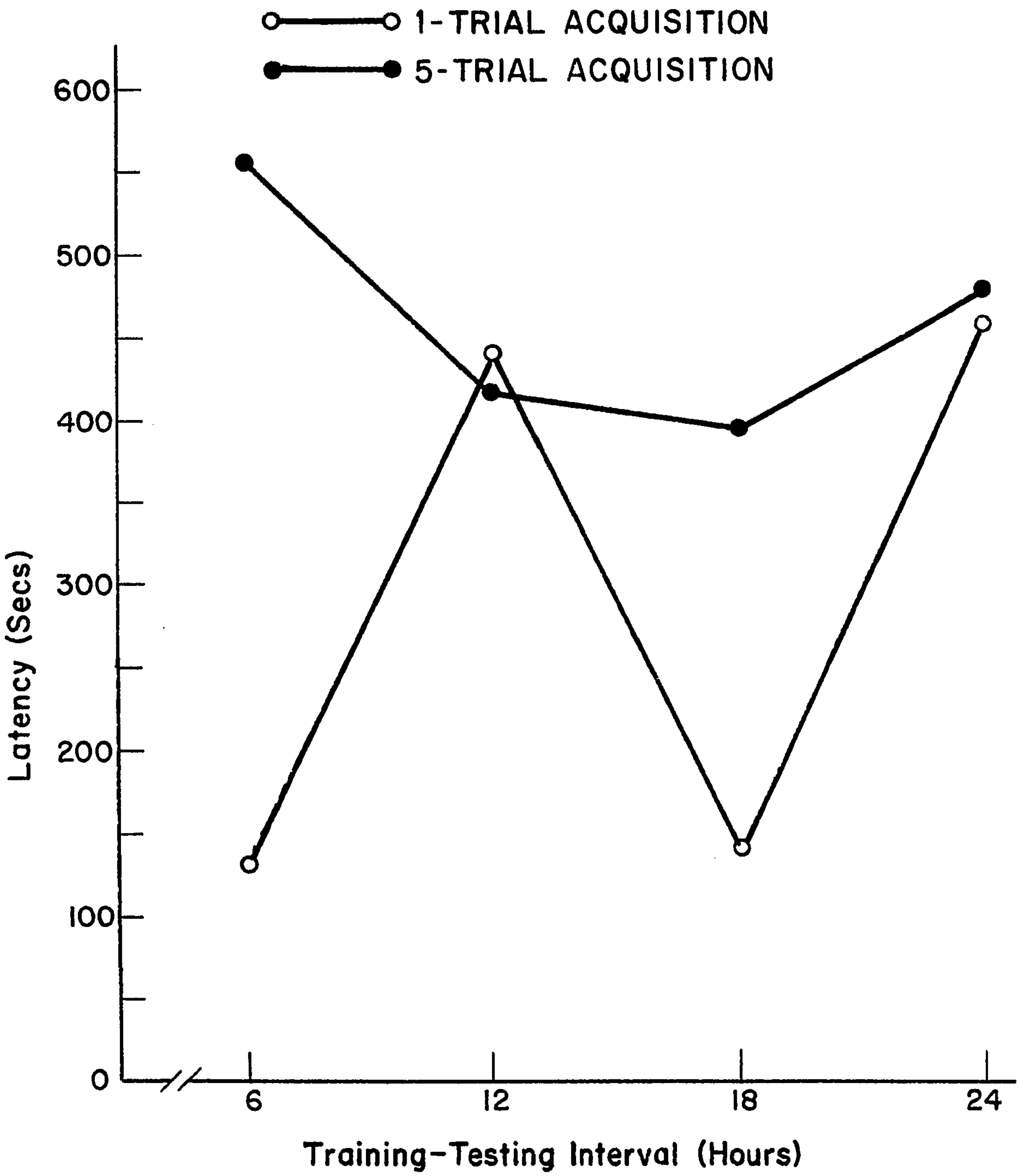
** $p < .01$

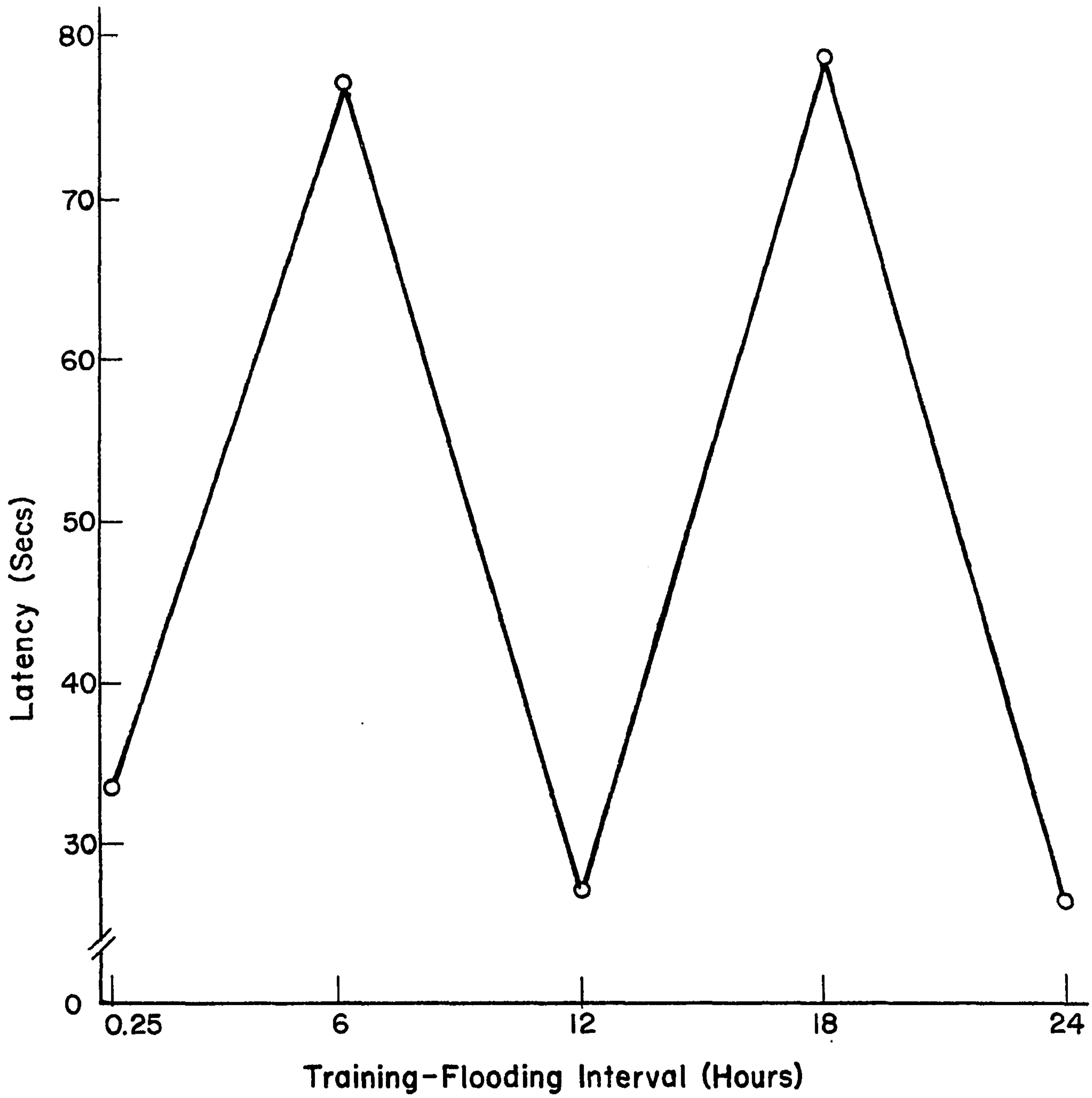
Figure Legend

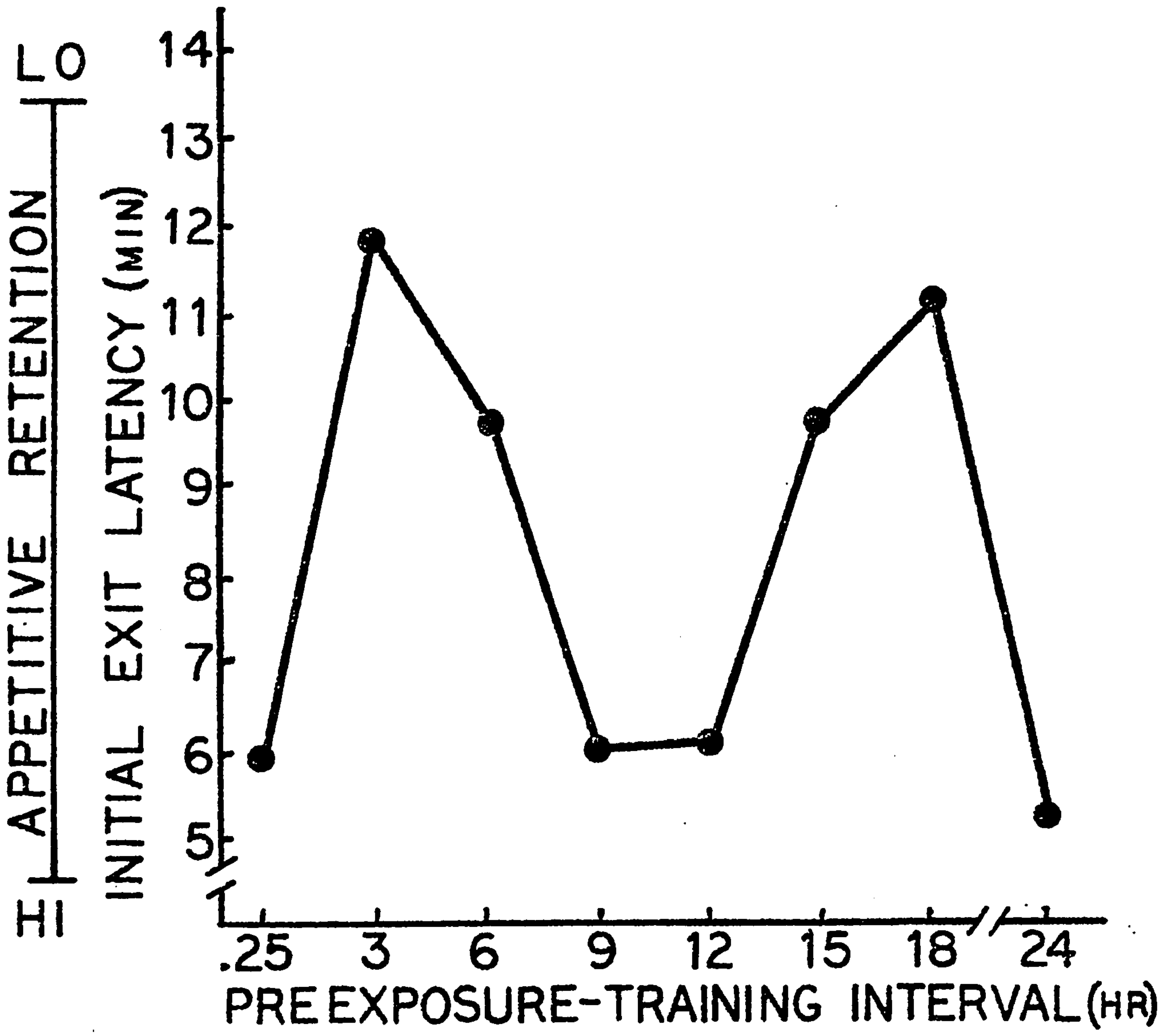
Figure 1. Mean testing step-through latencies for the 2 degrees of training groups at the 4 training-testing conditions.

Figure 2. Mean testing step-through latencies for the 5 acquisition-flooding groups.

Figure 3. Mean testing step-through latencies for the 8 preexposure-training interval treatments collapsed across the 2 preexposure periods.


1-TRIAL ACQUISITION
5-TRIAL ACQUISITION
Latency (Secs)
600
500
400
300
200
100
0
6
12
18
24
Training-Testing Interval (Hours)


80
70
60
50
40
30
0
Latency (Secs)
0.25
6
12
18
24
Training-Flooding Interval (Hours)



LO
HI
APPETITIVE RETENTION
INITIAL EXIT LATENCY (MIN)
14
13
12
11
10
9
8
7
6
5
.25
3
6
9
12
15
18
24
PREEXPOSURE-TRAINING INTERVAL (HR)

APPENDIX A

BACKGROUND

Background

The field of animal memory has undergone tremendous growth over the past two decades. This expansion has yielded a diversity of both animal memory research (e.g., biochemical changes associated with memory; brain lesions and memory; sequential factors in memory) and theoretical viewpoints (e.g., consolidation theory; state-dependent retrieval theories; interference theories). From this diversity a few tenets of memory are held in agreement by researchers in the field. One of the most widely endorsed assumptions is that retention of instrumental and Pavlovian conditioned responses is extremely persistent over time. This assumption is based on relatively few experimental findings. Skinner (1950) is often cited as demonstrating that pigeons can maintain an operant response over several years. Others reported persistent retention for Pavlovian conditioned responses (e.g., several years - Anderson, 1940) instrumental appetitive responses (e.g., 28 days - Gagne, 1941), and instrumental avoidance responses (e.g., 30 days - Hunter, 1935). It is also generally assumed that any retention loss which occurs is a monotonic function of the duration of disuse (Brush, 1971). This assumption is based on the early work in verbal learning which was pioneered by Ebbinghaus (1885).

Kamin (1957) reduced the generality of the latter assumption when he reported a curvilinear or U-shaped function of retention interval for the relearning of an avoidance response. Kamin administered 24 shuttlebox acquisition trials (incomplete learning) to 6 groups of rats and then, examined relearning (retention) by repeating the training procedure. The interval between acquisition and relearning was either 0, 0.5, 1, 6, or 24 h or 19 days. Retention declined from 0 to 1 h, then rose from 1 h to 19 days. There was no significant differences between retention at 0 and 19 days. Denny (1958) and Denny and Ditchman (1962) replicated Kamin's procedure and verified the U-shaped retention function (Kamin effect).

Since Kamin's original experiment, the U-shaped retention function has been obtained after a variety of training paradigms; one-way active avoidance (e.g., Anisman & Waller, 1971; Klein & Spear, 1970); discriminated active avoidance (e.g., Barrett, Leith, & Ray, 1971); passive avoidance (e.g., Denny & Thomas, 1960; Pinel & Cooper, 1966); signaled escape training (e.g., Brush, 1964; Pinel, 1968); classical fear conditioning (e.g., Bintz, Braud, & Brown, 1970; Walrath, 1968); and appetitive discrimination training (e.g., Tribhowan, Rucker, & McDiarmid, 1971). The interval of minimum retention is usually reported to be 1 h, although it has been found to vary up to 6 h after training (e.g., Spear, 1973).

Research examining the effect of original training on the Kamin effect, have usually found the effect to be characteristic of brief training periods or poorly learned responses. Anderson, Johnson, Schwendiman, and Dunford (1966) varied the training criteria of a two-way shuttlebox avoidance procedure with rats and examined retention during 40 retraining trials. Retention intervals of 0.08, 1, 4, and 24 h were used. they found the most pronounced Kamin effect following a 1-avoidance response criterion and either less pronounced or absent following 2 or 3 avoidance response criteria. Similar findings have been reported by Gabriel (1968) and Klein and Spear (1970). However, the results of another study indicated that as many as 100 avoidance training trials did not alter the pattern of the Kamin effect (Bruch & Sakellaris, 1968).

A number of theoretical interpretations of the Kamin effect have been forwarded. Kamin (1957) originally postulated two opposing retention processes which algebraically summate to produce the observed U-shaped retention function. He attributed the decline in retention from 0 to 1 h to forgetting, i.e., a continuing dissapation of positive transfer from original learning. A warm-up effect due to disruption of set and postural adjustments which becomes worse up to 1 h after training was suggested as the process responsible for forgetting. Kamin hypothesized that the rising segment of the curve (i.e., 1 h to 19 days) was due to an incubation effect, i.e., a progressive increase of subject's conditioned emotional response as a function of time after conditioning. In a later analysis, Kamin (1963) assumed the same monotonically increasing warm-up effect, but an inverted U function impeding performance (i.e., interference) which rises to a maximum 1 h after original training, instead of his earlier incubation of fear hypothesis.

Denny (1958) and later Denny and Ditchman (1962) postulated an incubation of anxiety (fear) explanation of the U-shaped function.

Presumably, anxiety intially increases in the interval immediately following the original learning trials to a point where it interfers with the act of shuttling. The peak of the incubation phase was assumed to be 1 h after training. Complete dissipation of anxiety to some preshock base level was assumed to occur within 24 h. Denny and Ditchman suggested recruited reticular activity as the physiological basis of incubation. This hypothesis has received support from other findings (e.g., Barrett, Leith, & Ray, 1971; McMichael, 1966; Steranka & Barrett, 1973). The incubation of fear hypothesis can only explain the Kamin effect under response activation procedures which involve shock.

Pinel and Cooper (1966) explained the U-shaped function for conditioned emotional and passive avoidance paradigms by the incubation of immobility. This explanation assumed more activity or less fear at intermediate retention intervals, which is the opposite of the incubation of fear interpretation. When animals receive shock in an apparatus and then are returned to the apparatus after different intervals, conditioned immobility was assumed to decline for the first hour and then increase markedly over the next 23 h. Since the performance of conditioned emotional and passive avoidance responses is enhanced by immobility, incubation of immobility will produce the U-shaped pattern of retention. Research by Bintz, Braud, and Brown (1970) and Pinel and Mucha (1973) supported by incubation of immobility hypothesis. This explanation is limited to explaining the Kamin effect under response suppression procedures.

Brush, Myer, and Palmer (1963) suggested a hypothesis based on a "parasympathetic over-reaction" following fear conditioning which peaks about one hour after training. Presumably, if the subject is returned to avoidance training at the peak of "parasympathetic over-reaction' they will be unable to cope with the stress of training. Brush et al. assumed sympathetic activity dominates avoidance training and in the process of restoring homeostasis during the retention interval, the autonomic nervous system overshoots to a state of parasympathetic dominance. This theory is dependent on fear conditioning paradigms which involve Pavlovian conditioning of fear.

The final explanation of the Kamin effect to be discussed here involves memory retrieval. Klein and Spear (1970) suggested that memory of the avoidance response is least efficiently retrieved at the 1 h interval. There basic argument was that by 1 to 4 h after acquisition many shock induced physiological changes have occurred (e.g., changes in ACTH level) which are not present at 0 h and have dissipated by 24 h. Thus, at intermediate test intervals poor avoidance is due to the presence of novel internal stimuli which were not previously associated with the response. This is essentially the process which has been proposed to explain the dissociation phenomenon, i.e., state-dependent learning, found in drug research (Overton, 1964). Spear, Klein, and Riley (1971) presented data which supported the state-dependent learning explanation of the Kamin effect. See Brush (1971) for a detailed review of the Kamin effect literature through 1970 for aversive conditioning paradigms.

Until recently, the Kamin effect was assumed to be a phenomenon peculiar to training procedures which employed aversive stimuli. Then, Tribhowan, Rucker, and McDiarmid (1971) found a U-shaped retention function following appetitive training. They trained rats for 18 trials on a three-choice discrimination apparatus with food reinforcement. After either 5 min, 1, 4, 8, or 24 h, the subjects were presented 18 trials of training with the discrimination reversed. Memory of the original discrimination was measured by errors on the reverse discrimination and was found to be a U-shaped function of intersession interval. The 4 h interval showed the least interference. Silvermen and Whitehouse (1974) trained rats in a Y-maze discrimination procedure with food reinforcement and reported a U-shaped retention function. They found a retention deficit associated with the 1 h interval, good performance at 24 h, and facilitated performance at 8 days. The results of the last two appetitive paradigms rule out incubation of fear or increased freezing as an explanation of the Kamin effect and lends support to memory processes or state-dependent learning interpretations. Contrary to the last two experiments, Hablitz and Braud (1972) found no Kamin effect for an incompletely learned approach response, and supported explanations based on fear.

A growing number of researchers are finding retention functions which are neither linear nor U-shaped, but which are phasic. Irwin and Benuazizi (1966) found a biphasic retention function in mice following one-trial passive avoidance training. They were studying the effects of strychnine and metrazol on the retention of one-trial passive avoidance learning. They included a saline injected control groups which is relevant here. Using intervals of 0, 5, 15, 30, and 90 min and 24 h, Irwin and Benuazizi found that retention, as indexed by response latency on trial 2, decreased rapidly from 0 to 5 min and then, increased from 5 to 90 min with a reversal of lesser magnitude from 90 min to 24 h. The first 90 min segment of the retention function is a U-shaped function similar to those reported earlier.

Cherkin (1971) reported a biphasic retention function following one-trial avoidance learning with chicks. Chicks will spontaneously peck an attractive target. During a single training trial, Cherkin suppressed the pecking by coating the target with a solution of methyl anthralinate and distilled water (aversive solution). Then, after either 10, 20, or 40 sec, 1.33, 2.67, 5.33, 10.67, 21.33, 42.67 min or 1.42, 2.84, 5.69, or 24 h, he tested retention (i.e., peck latency) with a dry target. This procedure is similar to the two chambered procedure used to condition one-trial passive avoidance in rats. Avoidance was maximal 10 sec after training, fell during the next 3 min., recovered to the initial level by 1.4 h, then declined to a pre-avoidance baseline by the 24 h interval. Cherkin proposed that the biphasic retention curve is compatible with a consolidation of memory theory. Specifically, the initial part of the curve is due to a rapid formation and decay of short-term memory followed by a slower formation and decay of long term memory.

The research discussed above utilized close approximations of Kamin's original training-testing intervals (TTIs) which do not represent a systematic sampling of TTIs within a 24 h period.

Holloway and Wansley (1973a) systematically varied the TTIs within a 24 h period and reported multiple retention deficits after one-trial passive avoidance. They placed albino rats on a light-dark cycle two weeks prior to training and kept them on it throughout the experiment. This light-dark cycle procedure was employed in all subsequent retention research from the Holloway laboratory. The subjects received a single training trial in a step-through passive avoidance task. The trial consisted of presenting the rat with 5 sec of 0.1 Watt footshock upon entering the darkened chamber of a two chambered apparatus. Half of the subjects were trained in the earlier portion of the light cycle and half in the latter portion. Passive avoidance was tested after one of 13 TTIs; 0.25, 6, 12, 18, 24, 30, 36, 42, 48, 54, 60, 66, or 72 h. Time of day in which training was administered was equated across and within the interval groups. Testing followed the same procedure as training except no shock. Retention performance was analyzed on the basis of initial step-through latencies during testing.

Holloway and Wansley found higher retention scores at 15 min or successive multiples of 12 h from the 6 h interval. The multiple retention deficits appeared to wane at longer intervals (i.e., 66 h) while the peaks remained the same out to the 72 h interval. The pattern of results was identical for the two different times of training. Mere exposure to the passive avoidance apparatus (no shock) had no effect on subsequent step-through latencies in the apparatus. Holloway and Wansley suggested an undetermined biological rhythmic process(es) effected retention performance or by the production of periodic state-dependent retrieval deficits as a result of fluctuations or shifts in organismic state at certain times after training. The latter explanation is an extended form of Klein and Spear's (1970) explanation of the Kamin effect.

In a later set of experiments, Holloway and Wansley (1973b) examined the role of circadian factors in the multiphasic retention function. They were also interested in replicating the finding under the same procedure (one-trial passive avoidance) and testing for its generality by employing a different procedure (multi-trial, one-way active avoidance). Training was administered at one of 4 times during the day (0300-0600 h, 0900-1200 h, 1500-1800 h, 2100-2400 h) and consisted of either one-trial passive avoidance or multi-trial, one-way active avoidance. The passive avoidance procedure was the same as described in their first experiment. The active avoidance apparatus was an automated, step-up device in which the subject could avoid 0.1 Watt footshock by climbing onto a platform which remained out for 15 sec before being retracted. Training retention was tested after either 0.25, 6, 12, 18, 24, or 48 h for both procedures. The number of trials to criterion (4 conditioned avoidance responses) was used as the retention measure for the active avoidance procedure.

Both the active and passive avoidance data demonstrated that the 0.25 and 24 h TTI groups had higher retention than the 6, 18, and 30 h TTI groups across the 4 training times, with the 12 h interval group being intermediate. These results replicated and extended their previous results. They hypothesized some undetermined constellation of periodically fluctuating internal events defined the state of the organism at the occasion of training and reinstatement of this training state became a relevant condition for optimal retrieval of the original conditioning. This explanation is similar to their previous explanation (Holloway & Wansley, 1973a).

Caul, Barrett, Thune, and Osborne (1974) failed to find a multiphasic retention function for an instrumental conditioning procedure at the TTI used by Holloway and Wansley. They trained rats in an automated Y-maze to escape or avoid shock by going to the lighted (safe) arm of the maze. Entry into the lighted arm within 10 sec successfully avoided 0.75 mA of footshock and initiated a 30 sec intertrial interval. Avoidance performance was assessed in independent groups of rats during a 50-trial test session which followed a 30-trial training session by 0.25, 1, 6, 12, 18, 24, or 30 h. The test trials were identical to the training trials. The number of correct avoidances, incorrect avoidances, correct escapes, and incorrect escapes were recorded during the training and testing sessions.

Caul et al. found a single decrement in avoidance performance at the 1 h interval with no differences between the other groups. This result follows the pattern of the Kamin effect and is contrary to Holloway and Wansley's (1973a, b) results. They also reported no decrements at any of the TTIs for their discrimination index (total correct avoidances and escapes) although the animals run at the 1 h TTI were more likely to make incorrect avoidances than animals run at other TTIs. Caul et al. interpreted this as reflecting a differential baseline of activity which is a function of time since the shock received during training, and is minimal 1 h after training. Thus, when testing follows the 1 h interval, the lower activity level decreases the subject's likelihood of learning the association between running and shock avoidance, and suggests that the U-shaped function is due to differential acquisition and not differential retention deficits. This interpretation is similar to Pinel and Cooper's (1966) incubation of immobility hypothesis discussed earlier. Holloway (1976) suggested that Caul et al. (1974) failure to find the multiphasic function may have been due to task differences. The salient stimulus (light) which governed responding in the Caul et al. study may have obscurred internal state factors which are necessary for state-dependent learning. Holloway (1976) also suggested that the U-shaped deficit and the multiphasic deficits may represent different processes.

Wansley and Holloway (1975b) examined retention performance in an appetitive task to test the generality of the multiple retention deficit phenomenon. Following 24 h of water deprivation, rats were administered a 10 min pretraining session to acquaint them with lick-tube drinking in a novel environment. The subjects were then water-deprived for 22 h 50 min, followed by 10 min free access to water in their home cage. One hour later training began in a new apparatus, irregular shaped maze or alley. Training consisted of a single trial in which the subject traversed the maze and licked the protruding water spout (5 sec access). Then, after 0.25, 1, 6, 12, 18, 24, 30, or 36 h, the subjects received a single trial under the same procedure as training. To minimize deprivation differences between the different interval groups, Wansley and Holloway gave all subjects in the 6, 12, 18, 24, 30, and 36 h groups a 10 min period of free access to water in their home cage beginning 1 h 10 min prior to testing. Latency to lick was their primary measure of performance.

The results characterized a multiphasic retention function which was similar to the results of their aversive paradigms (Holloway & Wansley, 1973a, b). Retention was higher for the 12, 24, and 36 h groups than for the 6, 18, and 30 h groups, while the 0.25, and 1 h groups were intermediate. A control experiment examined the importance of apparatus exposure in producing the multiphasic function by replicating the first procedure except for response contingent reinforcement during training. The rat's exposure to water after running the alley was delayed and given in a different apparatus. Under these conditions, the latency to enter the goalbox measure during testing was a linear or monotonic function with a decline across TTI groups. The results of these two experiments indicate that the 12 h oscillatory retention pattern has some degree of intertask generality and can be demonstrated without strong aversive stimuli (shock), although response contingent reinforcement is a crucial parameter. Wansley and Holloway invoked their previously discussed state-dependent retrieval hypothesis to explain the present results.

Jaffard, Destrade, Soumireu-Mourat and Cardo (1974) found improvement in retention of an appetitive discrimination task following intervals that typically yield multiple retention deficits. Seven groups of mice, which had been maintained on a 12 h light-dark cycle, were administered a 20 min session of discrimination training in which the discriminative stimulus was a light and buzzer presented simultaneously. Correct responding produced continuous food reinforcement. A second 10 min session was separated from the first by one of 7 intervals: 0, 5 min, 1, 3, 6, 12, and 24 h. Time of day of the sessions were counter-balanced between groups.

They found no differences in the second session discrimination ratio between the 0, 5 min, and 1 h groups; a significant increase in performance between 1 and 3 h which continued for the 6 and 12 h intervals; and an indistinguishable difference between 12 and 24 h intervals. Jaffard, et al. interpreted the results as supporting a consolidation hypothesis of retention. There are a number of differences between this study and other studies which have found multiple retention deficits (Wansley & Holloway, 1975b). They did not control deprivation differences between the different interval groups. Increased drprivation should produce greater arousal which may account for the superior performance at the longer intervals, or at least produce a confound between deprivation and retention. Furthermore, multiple retention deficits are usually found when the training period is brief and when strong external stimuli are absent. This experiment violated both of these conditions.

Holloway and Sturgis (1976) designed a procedure based on Capaldi's (1967) sequential theory of the partial reinforcement effect (PREE) to assess the nature of the assumed shift in internal state, endogenous vs training induced rhythmic process. According to sequential theory, the PREE is due to the conditioning of the memory of nonreinforcement (S^N) to a subsequent reinforced instrumental reesponse (R_I). Resistance to extinction is a function of the strength of this S^N-R_I association. Therefore, Holloway's state-dependent model of retention fluctuations predicts that the state of the organism during N-trials which preceed R trials should influence retrieval of S^N. Multiphasic fluctuations in the state following different N-R intertrial intervals should produce multiphasic fluctuations in the strength of the S^N-R_I associations as indexed by resistance to extinction.

The procedure consisted of training 5 independent groups of rats to escape 0.1 Watt footshock in a straight alley on a schedule of partial reinforcement. The sequence of the 15 acquisition trials was RRRN-RRRRN-RRRRN-R; where R refers to reinforced or escape trials and N refers to nonreinforced or nonescape trials. The interval between N and R trials varied across the groups, 0.25, 6, 12, 18, or 24 h, while the other intertrial intervals (ITI) were 30 sec. Twenty extinction trials (no shock) with a 30 sec ITI were given to all subjects 24 h prior to the last training trial. Resistance to extinction was measured during the extinction session. Holloway and Sturgis assumed that this procedure would minimize the effect of strict performance factors on retention performance, since the critical retention interval was different from the interval between exposure to the training procedure and testing.

Holloway and Sturgis reported greater resistance to extinction for the 0.25, 12, and 24 h N-R ITI groups than for the 6 and 18 h N-R ITI groups. This data supported their hypothesis that some endogenous, cyclically determined state of the organism modulates the accessibility of S^N on R trials and leads to similar fluctuations in the strength of the S^N-R_I association depending on the interval between N and R trials. A shock induced rhythmic process can not account for the results because the subjects were shocked on both N and R trials and the interval between shock exposure and testing differed from the critical interval between N and R trials.

In a second study concerned with the processes underlying the assumed shift in internal state, Holloway (1976) examined the effects of interpolated-shock on relearning. Ten groups of rats were trained in the step-up active avoidance task previously described (Holloway & Wansley, 1973b). Five groups were tested 24 h later (a TTI which usually produced superior retention) and 5 groups were tested 30 h later (a TTI which usually produced inferior retention). Subgroups of subjects received either noncontingent shock in an apparatus dissimilar to the training apparatus or in the training apparatus at one of 5 intervals following training; 0.25, 6, 12, 18, or 23.75 h. Holloway reasoned that a shock induced explanation of the physiological flucutations would predict a second shock event to reset the fluctuations. Therefore, interpolated shock at 6 or 18 h should impair retention in the 24 h TTI groups relative to the groups receiving interpolated shock 0.25, 12, or 23.75 h after training. Furthermore, the usual retention deficit at the 30 h TTI should be mitigated in those groups receiving shock 6 and 18 h after training. A pretraining endogenous rhythmic explanation of the fluctuations would predict an interaction between interpolated shock and retention performance only for those groups receiving interpolated shock when retention performance is high (i.e., 0.25, 12, and 23.75 h).

The results of the 24 h TTI groups indicated that interpolated shock at 0.25, 12, and 23.75 h impaired retention performance relative to interpolated shock at 6 and 18 h after training. Retention performance in the 30 h TTI groups was uniformly poor. Retention performance and interpolated shock only interacted when retention was high (i.e., 0.25, 12, & 24 h). Holloway concluded that the results supported the hypothesis that a pretraining rhythmic process becomes associated with original training and is required for access to the training experience.

Wansley and Holloway (1975a) examined the effect of lesioning the suprachiasmatic nucleus of the hypothalamus on the multiple retention deficit phenomenon. The suprachiasmatic nucleus receives direct input from the primary visual pathway and is believed to be essential for circadian fluctuations in such behaviors as eating, drinking and spontaneous activity (Rusak & Zucker, 1975). They collected baseline data on eating, drinking and activity before and after making a bilateral discrete radio frequency lesion of the nucleus in rats. The lesion procedure eliminated the 3 circadian rhythmic fluctuations. Approximately 1.5 weeks after surgery, they trained the subjects in the same active or passive avoidance procedures as described in an earlier study (Holloway & Wansley, 1973b) and examined retention performance after 0.25, 6, 12, 18, and 24 h.

Wansley and Holloway found a single retention deficit at the 6 h interval after both training tasks for the lesioned subjects. A non-lesioned control group demonstrated the typical multiple retention deficits following either training task. These data supported their assumption that the multiphasic retention function is based on some biological rhythmic process(es). The U-shaped pattern of the lesioned subject's retention results prompted Wansley and Holloway to suggest that the initial deficit (Kamin effect) may be produced by processes other than those controlling the multiphasic retention phenomenon.

A few general principles emerge from the research discussed in this review. The pattern of the retention function across time is typically dependent on the TTIs included in the study. Twenty-four hour TTIs yield monotonic retention functions: Kamin-type (1957) TTIs (0.5, 1, 6, and 24 h and 19 days) yield U-shaped retention functions; successive 6 h TTIs yield multiphasic retention functions. Since the multiphasic retention function is based on the most systematic sampling of TTIs, it may be assumed to represent the most accurate description of retention performance across time within the boundary conditions to be specified below. Wansley and Holloway (1975a) suggested that the U-shaped and multiphasic retention fluctuations may involve different underlying processes. Furthermore, a systematic sampling of TTIs within a 6 h period of time may result in yet another retention pattern. Althoug the U-shaped and multiphasic functions have been found across a number of different training paradigms (e.g., appetitive instrumental conditioning, active avoidance), retention deficits have been reported most often when the learning period is brief (e.g., one-trial passive avoidance, incomplete shuttlebox avoidance) and when there is a minimum of salient external stimuli governing the responding (e.g., passive avoidance; step-up avoidance). U-shaped and cyclical multiphasic retention functions have been found for rats; while irregular biphasic retention functions have been reported for mice and chicks (Irwin & Benuazizi, 1966 and Cherkin, 1971, respectively). Holloway (1975) suggested that a 12 h light-dark cycle may be necessary for the multiphasic retention function. Finally, shock related explanations of the retention deficit(s) can not account for deficits found after appetitively motivated training. Holloway's state dependent retrieval theory can explain the deficit(s) across these two training procedures.

References

Anderson, A. C. Evidences of reminiscence in the rat in maze learning. Journal of Comparative and Physiological Psychology, 1940, 30, 399-412.

Anderson, A. C., Johnson, L., Schwendiman, G., & Dunford, G. Retention of an incompletely learned avoidance response: Some problems with replication. Psychonomic Science, 1966, 6, 23-24.

Anisman, H. & Waller, T. G. Effects of conflicting response requirements and shock compartment confinement on the Kamin effect in rats. Journal of Comparative and Physiological Psychology, 1971, 77, 234-239.

Barrett, R. J., Leith, N. J., & Ray, O. S. Kamin effect in rats: Index of memory or shock induced inhibition. Journal of Comparative and Physiological Psychology, 1971, 77, 240-244.

Bintz, J., Braud, W. G., & Brown, J. S. An analysis of the role of fear in the Kamin effect. Learning and Motivation, 1970, 1, 170-176.

Brush, F. R. Avoidance learning after fear conditioning and unsignalled shock. Psychonomic Science, 1964, 1, 405-406.

Brush, F. R. Retention of aversively motivated behavior. In F. R. Brush (Ed.) Aversive learning and conditioning. New York: Academic Press, 1971.

Brush, F. R., Myer, J. S., & Palmer, M. E. Joint effects of inter-trial and intersession interval upon avoidance learning. Psychological Reports, 1964, 14, 31-37.

Brush, F. R., & Sakellaris, P. C. Extinction as a function of time after avoidance training. Paper presented at the meeting of the Psychonomic Society, St. Louis, Missouri, October, 1968.

Capaldi, E. J. A sequential hypothesis of instrumental learning. In K. W. Spence and J. T. Spence (Eds.), The psychology of learning and motivation: advances in research and theory (Vol. 1). New York: Academic Press, 1967.

Caul, W. F., Barrett, R. J., Thune, G. E., & Osborne, G. L. Avoidance decrement as a function of training-testing interval: Single cycle or multiphasic? Behavioral Biology, 1974, 11, 409-414.

Cherkin, A. Biphasic time course of performance after one-trial avoidance training in the chick. Communications in Behavioral Biology, 1971, 5, 379-381.

Denny, M. R. The "Kamin-effect" in avoidance conditioning. Paper presented at the meeting of the American Psychological Association, Washington, D. C., September, 1958.

Denny, M. R., & Ditchman, R. E. The locus of maximal "Kamin Effect" in rats. Journal of Comparative and Physiological Psychology, 1962, 55, 1069-1070.

Denny, M. R., & Thomas, J. O. Avoidance learning and relearning as a function of shuttlebox dimensions. Science, 1960, 132, 620-621.

Ebbinghaus, H. Das Gedactnis: Untersuchungen zur experimentellen psychologie. Leipzig: Duncker & Humboldt, 1885.

Gabriel, M. Effects of intersession delay and training level on avoidance extinction and intertrial behavior. Journal of Comparative and Physiological Psychology, 1968, 66, 412-416.

Gagne, R. M. The retention of a conditioned operant response. Journal of Experimental Psychology, 1941, 29, 296-305.

Hablitz, J. J., & Braud, W. G. Adrenalin, sodium amobarbital, and the Kamin effect in albino rats. Learning and Motivation, 1972, 3, 151-158.

Holloway, F. A. Non-monotonic temporal gradients reflecting susceptibility of learned responses to interference. Submitted for publication, 1976.

Holloway, F. A., & Sturgis, R. D. Periodic decrements in retrieval of memory of non-reinforcement reflected in resistance to extinction. Submitted for publication, 1976.

Holloway, F. A., & Wansley, R. A. Multiphasic retention deficits at periodic intervals after passive avoidance learning. Science, 1973, 180, 208-210. (a)

Holloway, F. A., & Wansley, R. A. Multiple retention deficits at periodic intervals after active and passive avoidance learning. Behavioral Biology, 1973, 2, 1-14. (b)

Hunter, W. S. Conditioning and extinction in the rat. British Journal of Psychology, 1935, 6, 135-148.

Irwin, S., & Benuazizi, A. Pentylenetetrazol enhances memory function. Science, 1966, 152, 100-102.

Jaffard, R., Destrade, C., Somireu-Mourat, B., & Cardo, B. Time-dependent improvement of performance on appetitive tasks in mice. Behavioral Biology, 1974, 11, 89-100.

Kamin, L. J. Retention of an incompletely learned avoidance response. Journal of Comparative and Physiological Psychology, 1957, 50, 457-460.

Kamin, L. J. Retention of an incompletely learned avoidance response: Some further analyses. Journal of Comparative and Physiological Psychology, 1963, 56, 713-718.

Klein, S. B., & Spear, N. E. Forgetting by the rat after intermediate intervals ("Kamin effect") as retrieval failure. Journal of Comparative and Physiological Psychology, 1970, 71, 165-170.

McMichael, J. S. Incubation of anxiety and instrumental behavior. Journal of Comparative and Physiological Psychology, 1966, 71, 208-211.

Overton, D. A. State-dependent or "dissociated" learning produced with pentobarbital. Journal of Comparative and Physiological Psychology, 1964, 57, 3-12.

Pinel, J. P. Evaluation of the one-trial passive avoidance task as a tool for studying ECS-produced amnesia. Psychonomic Science, 1968, 13, 131-132.

Pinel, J. P., & Cooper, R. M. Demonstration of the Kamin effect after one-trial avoidance learning. Psychonomic Science, 1966, 4, 17-18.

Pinel, J. P., & Mucha, R. F. Incubation and Kamin effects in the rat: changes in activity and reactivity. Journal of Comparative and Physiological Psychology, 1973, 84, 661-668.

Spear, N. E. Retrieval of memory in animals. Psychological Review, 1973, 80, 163-194.

Spear, N. E., Klein, S. B., & Riley, E. P. The Kamin effect as "state-dependent" learning: Memory retrieval failure in the rat. Journal of Comparative and Physiological Psychology, 1971, 74, 416-425.

Steranka, L. R., & Barrett, R. J. Kamin effect in rats: Differential retention or differential acquisition of an active-avoidance response? Journal of Comparative and Physiological Psychology, 1973, 85, 324-330.

Tribhowan, T., Rucker, W. B., & McDiarmid, C. G. Demonstration of the Kamin like effect after appetitive training. Psychonomic Science, 1971, 23, 41-42.

Walrath, L. C. Interference of avoidance in rabbits. Unpublished manuscript, 1968. Cited by F. R. Brush, Retention of aversively motivated behavior. In F. R. Brush (Ed) Aversive learning and conditioning, New York: Academic Press, 1971.

Wansley, R. A., & Holloway, F. A. Lesions of the suprachiasmatic nucleus (hypothalamus) alter the normal retention performance in the rat. Neuroscience Abstracts, 1975, 1, 810 (abstract). (a)

Wansley, R. A., & Holloway, F. A. Multiple retention deficits following one-trial appetitive training. Behavioral Biology, 1975, 14, 135-149. (b)

APPENDIX B

STATISTICAL TABLES

Experiment I

Analysis of Variance on Testing Step-Through Latencies

Source	df	MS	F
A (Degree of Training)	1	287296	5.69*
B (Acquisition Time)	1	150350	2.98
C (Acauisition-Testing Interval)	3	138459	2.75*
AB	1	6683	0.13
AC	3	93936	1.86
BC	3	6577	0.13
ABC	3	5936	0.11
Error	48	50482	

*$p < .05$

Experiment II

Analysis of Variance on Testing Step-Through Latencies

Source	df	MS	F
A (Degree of Exposure)	1	292.9	10.1**
B (Training Time)	1	14.9	0.5
C (Training-Testing Interval)	1	20.9	0.7
AB	1	17.6	0.5
AC	1	8.1	0.3
BC	1	2.5	0.1
ABC	1	9.4	0.3
Error	24	29.0	

**$p < .01$

Experiment III

Analysis of Variance on Testing Step-Through Latencies

Source	df	MS	F
Between (Acquisition-Flooding Interval)	4	5956.8	4.76**
Within	35	1251.3	

$p < .01$

Experiment IV

Analysis of Variance on Step-Through Latencies

ACQUISITION TRIAL

Saource	df	MS	F
A (Preexposure Time)	1	0.18	0.02
B (Preexposure-Acquisition Interval)	7	62.09	7.35**
AB	7	4.06	0.48
SS/AB	56	8.45	

**$p < .01$

TESTING TRIAL

Source	df	MS	F
A (Preexposure Time)	1	1.02	0.46
B (Preexposure-Acquisition Interval)	7	0.87	0.39
AB	7	1.17	0.53
SS/AB	56	2.21	