

TRAINING OF CONDITIONED ENHANCEMENT AND CONDITIONED SUPPRESSION IN RATS

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Abstract. Stable conditioned enhancement of barpressing in rats was elicited by darkness stimulus signaling continuous food reinforcement (CRF) component of a multiple schedule in which 2.5 min variable interval reinforcement (VI) constituted the second component. Conditioned enhancement was rapidly acquired and resistant to extinction. In some groups concurrent alimentary and defensive training was conducted in which darkness signaled food CRF and acoustic white noise signaled inescapable foot shock, both presented against the 2.5 min VI food reinforcement schedule. The continuous reinforcement schedule and/or conditioned enhancement showed a decremental effect on conditioned suppression, but only when defensive trials were less frequent than trials with continuous reinforcement of barpresses. Residual enhancement of barpressing after termination of the stimulus eliciting conditioned enhancement, observed at early stages of training, was then changed to a slight decrease of the barpressing rate. Opposite changes were observed after the offset of the stimulus eliciting conditioned suppression. Changes in intertrial response rates are considered as reflecting the summation of stimuli possessing opposite motivational values.

INTRODUCTION

The Estes-Skinner's conditioned emotional response (CER) paradigm (10) consists in suppression of the on-going barpressing for food, or any other appetitively reinforced instrumental responding, by a fear evoking conditioned stimulus

(CS). This property of the CS is acquired in the course of defensive classical conditioning in which CS termination coincides with termination of a brief inescapable shock. However, as shown in a recent review (29), in many studies using the CER paradigm the conditioned enhancement of the on-going instrumental responding has also been observed. Generally, stimuli that explicitly signal the nonoccurrence of shock may accelerate on-going appetitively reinforced instrumental responding. Conditioned stimuli acquire this response enhancement property after such Pavlovian procedures as experimental extinction (3), prolonged training enabling the development of inhibition of delay (13, 22), varieties of differentiation learning (2, 7, 8, 12, 15, 25, 26, 33, 34), and also after training of the conditioned inhibitor (29–32).

Since CER studies typically focus attention on conditioned suppression, the phenomenon of conditioned enhancement has not been investigated sufficiently. In some CER experiments involving Pavlovian inhibitory training, the acceleration of responding has not been observed, but neither the conditions necessary for manifesting response enhancement, nor the possible explanations of this phenomenon were extensively discussed. One theoretical alternative is that stimuli signaling a negative contingency with shock, in the process of differential conditioning become security stimuli and elicit conditioned relief responses. Due to the antagonistic interactions between centers modulating fear and relief response (9, 17), security stimuli suppress the residual fear response that has been conditioned to the entire experimental context and allow a high rate of instrumental responses. Another line of reasoning is related to numerous observations indicating that fear does not suppress completely appetitively motivated responding of hungry rats, and after sufficient training a subject's behavior reduces the opportunities for appetitive reinforcement only to a certain degree (28). Thus, the accelerated barpressing during the action of a CS signaling the absence of shock may be considered a compensatory response. Therefore, the greater suppression during presentations of stimuli signaling shock, the more the enhancement during stimuli signaling absence of shock.

The question of interrelations between conditioned suppression and conditioned enhancement is linked to a more general problem. It was asked in theoretical (9) and experimental (29) papers, whether in situations where an organism is under the influence of opposite motivations, stimuli acquiring inhibitory properties for one response pattern will simultaneously acquire excitatory properties for the opposite response. The answer to this question may be important for studies of learning in complex situations (9).

The present study approaches the problem of the interactions between conditioned enhancement and conditioned suppression from another side. A high rate of barpressing may be obtained using continuous reinforcement signaled by a stimulus occasionally presented in an experimental context in which intermittent

food reinforcement schedule is in effect. This type of experimental context is homogeneous because only one kind of unconditioned stimulus, i. e. food reinforcement, is used. In contrast, when defensive conditioning takes place in the same experimental situation, the context is of a mixed character. The aim of the present study was to trace the course of differentiation learning based on continuous versus intermittent food reinforcement in both homogeneous and heterogeneous experimental contexts. It was expected that the antagonistic relations between the alimentary and defensive behavioral systems will influence the learning process and the stability of acquired differential high rates of barpressing to the stimulus signaling continuous food reinforcement.

MATERIAL AND METHODS

Subjects were 56 naive male hooded rats, all from the same colony and approximately 3 months old at the start of the experiments. The apparatus consisted of eight modified Skinner boxes, each containing an electrifiable grid floor and a single bar on one of the walls with a food-tray under it. A pilot light centered on the top of the back chamber wall provided illumination in the vicinity of the bar equal to 205 ± 5 lx. Equipment for automatic programming and recording of the experiment was located in an adjoining room.

Before the experiments, all rats were reduced to 75% of their ad. lib. body weight and were maintained of that weight throughout the investigation. During the experiments a 22 h schedule of food deprivation was applied. Sessions started every day at the same time for a given subject, and daily portions of food were given just after each experimental session. Preliminary training consisted of initial presentation of 40 "free" 45 mg food pellets on a 1 min variable interval (VI) schedule of reinforcement (magazine training), followed immediately by a period with continuous reinforcement of barpresses until 120 food pellets were delivered in a single session. Then five daily 2 h sessions of barpressing under a 2.5 min VI schedule of food reinforcement were given which resulted in the acquisition of stable on-going barpressing behavior for food. During the last day, called Dummy Day (*D*-day), and during all subsequent sessions, the numbers of barpresses emitted in consecutive 30 s periods were counted. The 2.5 min VI schedule of food reinforcement was in effect during all subsequent stages of the experiments, i. e., all contingencies employed during the following stages of the experiments were superimposed on the 2.5 min VI food reinforcement schedule.

This paper presents results of two experiments from a longer series. Within each experiment, rats were divided into several groups at the beginning of barpress training. The groups, 8 rats each, differed from each other in the number of alimentary and defensive trials presented during each session and also in the testing procedures employed after the acquisition stage was completed. Conditioned sti-

muli were presented for 1 min. Depending on the group, there were four, six or eight trials within a 2 h session. The times of the trial onsets for these cases are illustrated in Fig. 1.

In each experimental group, preliminary training was followed by two Pretest Days (*P*-day), during which to-be-conditioned stimuli (darkness or 70 dB white

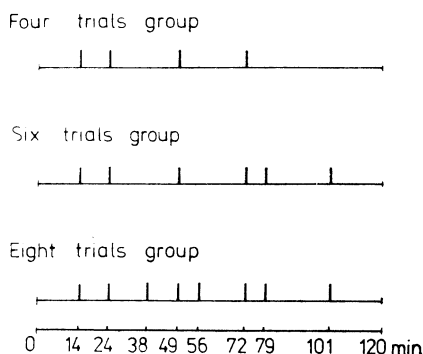


Fig. 1. The times of the trial onsets during 2 h sessions.

noise) were presented alone at appropriate times in the session for 1 min periods during which there were no other changes in the experimental procedure. The next stage of the experiments consisted of seven days of conditioning. In Alimentary Groups of both experiments, four 1 min darkness periods were used as the alimentary conditioned stimulus (CS_{alim}), and during the action of CS_{alim} each barpress was reinforced by a food pellet. Thus, the CS_{alim} signaled continuous food reinforcement (CRF) schedule. In Alimentary-Defensive Groups two kind of trials were presented. Darkness periods of 1 min served as the CS_{alim} signaling continuous reinforcement for food, whereas a 1 min presentations of 70 dB white noise served as the defensive stimulus (CS_{def}), which terminated with 1 s of inescapable scrambled electric shock of 2 mA intensity. Group denotations indicate numbers of CS_{alim} and CS_{def} presentations during each conditioning session. As shown in Table I, the Experiment I included Group 4-0 (four CS_{alim} and no CS_{def}), Group 4-2 (four CS_{alim} and two CS_{def}), Group 2-2 (two CS_{alim} and two CS_{def}), and Group 0-0 (neither CS_{alim} nor CS_{def}) serving as a control. The Experiment II included Group 4-0 (four CS_{alim} and no CS_{def}), Group 4-2 (four CS_{alim} and two CS_{def}), and Group 4-4 (four CS_{alim} and four CS_{def}).

The order of CS_{alim} and CS_{def} presentations was predetermined and changed each day. For the case of two alimentary and two defensive trials (Group 2-2; Experiment I), the arrangements were:

1. CS_{def} , CS_{alim} , CS_{def} , CS_{alim} ;
2. CS_{alim} , CS_{def} , CS_{alim} , CS_{def} .

Arrangement 1 was used on uneven days and Arrangement 2 was used on even days.

For the case of four alimentary and two defensive trials (Groups 4-2 of Experiment I and Experiment II) the arrangements on consecutive days of training were:

1. CS_{alim} , CS_{def} , CS_{alim} , CS_{alim} , CS_{def} , CS_{alim} ;
2. CS_{def} , CS_{alim} , CS_{alim} , CS_{def} , CS_{alim} , CS_{alim} ;
3. CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{alim} ;
4. CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{alim} ;
5. CS_{alim} , CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} ;
6. CS_{def} , CS_{alim} , CS_{alim} , CS_{def} , CS_{alim} , CS_{alim} .

During consecutive experimental sessions stimuli arrangements were repeated in the same order from 1 to 6 for all rats of these experimental groups.

For the case of four alimentary and four defensive trials during each session (Group 4-4; Experiment II), the following arrangements were used consecutively:

1. CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{def} ;
2. CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} ;
3. CS_{alim} , CS_{def} , CS_{def} , CS_{alim} , CS_{alim} , CS_{def} , CS_{alim} , CS_{def} ;
4. CS_{def} , CS_{alim} , CS_{alim} , CS_{def} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} ;
5. CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{def} , CS_{alim} ;
6. CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{def} , CS_{alim} , CS_{alim} , CS_{def} .

In Experiment II, after the conditioned training in all experimental groups an acute extinction procedure for CS_{alim} was introduced, wherein the darkness CS was given at the 14th min of the session and lasted for 60 min without the CRF schedule for food, however, the 2.5 min VI schedule was in effect. Ten consecutive 2 h extinction sessions were given. There was no CS_{def} presentation during this stage of the experiment.

The magnitude of changes in barpressing rate during CS_{alim} and CS_{def} presentations was measured by computing the „suppression ratio” $B/(A + B)$ described by Annau and Kamin (1), where B represents the number of barpresses emitted during the 1 min action of the CS (CS_{alim} or CS_{def}) and A is the number of response during the 1 min period immediately before the CS onset. To evaluate the immediate effect of CS termination on the on-going behavior, the numbers of barpresses emitted during 1 min intervals after CS_{alim} or CS_{def} offset were collected (the C score) and compared with the rate of responding before CS_{alim} or CS_{def} onset, using the formula $C/(A + C)$. Additionally, daily suppression ratios were computed for each rat by summing responses emitted during the appropriate intervals of a given kind of trials. In Group 0-0 of the Experiment I, the numbers of barpresses were collected and „dummy” suppression ratios were computed for those periods corresponding to CSi presentations in the other groups.

RESULTS

Pretest Days. The introduction of the stimuli used later in the conditioning training evoked some changes in on-going barpressing behavior. Generally, the darkness had a stronger disruptive effect than the 70 dB white noise. For each presentation of the stimuli in a given experimental group, the numbers of barpresses emitted before and during action of the stimuli were compared using the Wilcoxon matched-pairs two-tailed test (A-B index)¹. These analyses showed that the darkness stimulus in eight percent of the presentations elicited suppression ($P < 0.05$,

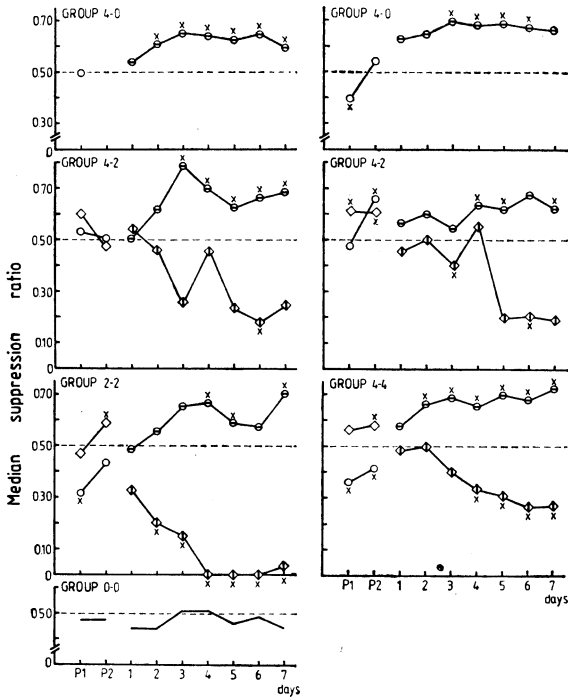


Fig. 2. Median daily enhancement and suppression ratios during *P*-days and conditioned training for each group of Experiment I (left panel) and Experiment II (right panel). Circles denote the darkness CS and circles with a horizontal bar indicate the darkness CS signaling continuous food reinforcement for bar presses. Diamonds denote the 70 dB white noise CS and diamonds with a vertical bar indicate the 70 dB white noise presented with the shock US. For Group 0-0 of Experiment I "dummy" ratios were estimated using data from intervals corresponding to pre-CS and CS periods in other groups. Crosses below or above the symbols for daily ratios denote suppression or enhancement levels that were respectively significant at $P < 0.05$ or better, as estimated by A-B comparisons (Wilcoxon tests).

¹ Due to failure of the print-out counter some data from the P_2 -day in Group 4-0 of the Experiment I were missed, thus they were neither taken into account for calculations nor presented in Fig. 1.

or better) and in six percent of presentations resulted in enhancement of barpressing. In contrast, the 70 dB white noise never produced significant suppression and in 23 percent of cases elicited enhancement of barpressing. Consistent with our previous observations (3, 15, 16, 30) suppression occurred with the earlier presentations, reflecting an orienting reaction, whereas enhancement was observed later, after habituation of this orienting response. The marked unconditioned effect of the darkness stimulus on barpressing behavior was the reason for using two Pre-test Days in previous experiments (32) and in this study.

It is worth mentioning that comparisons of the numbers of barpresses emitted in Group 0-0 of Experiment I on *P*-days during time intervals corresponding to the stimulus periods of the experimental groups revealed no significant changes of barpressing rate. Similar lack of changes were found in each experimental group during the *D*-day, the last day of preliminary training prior to the first *P*-day.

Training of conditioned enhancement and conditioned suppression. The results of the conditioning procedures in terms of median daily enhancement and suppression ratios are presented in Fig. 2 for each experimental group. As seen from the Figure, the contingency signaled by the CS_{alim} was quickly detected by rats, and after brief training elicited enhancement of barpressing behavior. By the second day of training the daily $B/(A + B)$ ratios estimated for CS_{alim} presentations exceeded the 0.6 value in all groups and were maintained to the end of this stage of the experiments. Analyses by the Wilcoxon matched-pairs two-tailed test (*A-B* index) revealed some between-group differences, but the general impression is that enhancement of barpressing was fairly stable across rats within most of the experimental groups. As far as acquisition of conditioned suppression to the CS_{def} is concerned, smooth learning curves were observed in Group 2-2 of Experiment I and Group 4-4 of Experiment II, whereas retarded acquisition of the defensive response was found in Groups 4-2 of both experiments with marked fluctuations of the median daily suppression ratios.

Additional information concerning the effectiveness of conditioning, based on *A-B* indices estimated for individual trials, is presented in Table I. The first statistically significant enhancement of barpressing to the CS_{alim} was observed earlier than the first significant suppression to the CS_{def} . The only exception was Group 2-2 of Experiment I in which there were two not four presentations of the CS_{alim} during the experimental session. This group was also marked by a large percentage of defensive trials in which significant suppression was observed. In other groups instances of significant enhancements to the CS_{alim} were at least two times more frequent than instances of significant suppression to the CS_{def} . Generally, the data presented in Table I indicate more successful acquisition of enhancement as a result of continuous food reinforcement of barpresses emitted during CS_{alim} action than acquisition of suppression by pairing CS_{def} with inescapable shock.

It should also be mentioned that the changes in barpressing rates conditioned to the CS_{alim} and to the CS_{def} were just opposite to the unconditioned effects of

TABLE I

Some indices of the conditioning process. *A*, indicates numbers of trials presented in each session; *B*, shows the first consecutive trial of a given kind in which significant change in barpressing rate, enhancement to CS_{alim} or suppression to CS_{def}, occurred; *C*, indicate percent of trials of a given kind in which significant changes in barpressing rate were observed

Group	A		B		C	
	CS _{alim}	CS _{def}	CS _{alim}	CS _{def}	CS _{alim}	CS _{def}
Experiment I						
Group 4-0	4	—	3rd	—	67.8	—
Group 4-2	4	2	7th	11th	53.6	14.3
Group 2-2	2	2	5th	4th	50.0	78.6
Group 0-0	—	—	—	—	—	—
Experiment II						
Group 4-0	4	—	4th	—	46.4	—
Group 4-2	4	2	7th	9th	46.4	21.4
Group 4-4	4	4	4th	9th	75.0	25.0

the darkness and the 70 dB white noise observed during the *P*-days. Moreover, the first presentation of darkness during the first conditioning session evoked significant suppression of the barpressing in Group 4-2 of Experiment I and in Group 4-4 of Experiment II. During the first conditioning session in the same groups the last presentation of 70 dB white noise still elicited significant enhancement of barpressing. These unconditioned effects were then overcome in the course of training, and the data from Table I indicate that alimentary conditioning was also more successful in these groups than defensive conditioning.

Daily enhancement and suppression ratios were analyzed by ANOVA tests. For Group 0-0 of the Experiment I data from intervals corresponding to pre-CS and CS periods in other groups (so called dummy trials) were used. The two-way ANOVA based on the daily ratios for CS_{alim} presentation in all groups showed significant effect of groups ($F_{3/28} = 10.38$, $P < 0.001$) and days ($F_{6/168} = 8.89$, $P < 0.001$), but not significant interaction ($F_{18/168} = 1.60$, $P > 0.05$). Further Duncan comparisons revealed that the group effect was due to Group 0-0, which differed from all other groups (P 's < 0.01) while other differences were not significant. The mean daily enhancement ratio for Group 0-0 was 0.495 indicating no change in barpressing rate as contrasted with 0.605, 0.648, and 0.618 for Groups 4-0, 4-2 and 2-2, respectively. The largest enhancement effects were observed during the 3rd and the 4th conditioning sessions, but daily ratios during the 1st conditioning session differed significantly from those in all subsequent sessions (P 's < 0.01). The ANOVA for Experiment II, in which there was no control group, yielded only a day effect ($F_{6/126} = 2.84$, $P < 0.025$) with mean daily enhancement ratios of 0.641, 0.620, and 0.669 for Group 4-0, Group 4-2, and Group 4-4 respectively.

The exceptionally successful defensive conditioning in Group 2-2 of Experi-

ment I was confirmed by an ANOVA based on daily suppression ratios estimated for CS_{def} presentations which showed group ($F_{1/14} = 10.61$, $P < 0.01$) and day effects ($F_{6/84} = 5.87$, $P < 0.001$). Mean daily suppression ratios from all seven days of conditioning were 0.375 in Group 4-2 and 0.156 in Group 2-2 of Experiment I. A similar ANOVA of Experiment II showed no effect of groups but significant effect of days ($F_{6/84} = 9.39$, $P < 0.001$) and interaction ($F_{6/84} = 2.82$, $P < 0.05$). The mean daily suppression ratios were 0.375 and 0.340 for Group 4-2 and Group 4-4 of Experiment II, respectively. Duncan comparisons revealed more rapid acquisition of suppression in Group 4-4 with the largest between-groups differences observed during the 4th conditioning session ($P < 0.05$).

Experiment I was conducted in late autumn, and Experiment II in early spring, so that these seasonal differences may have affected the magnitudes of conditioned suppression and enhancement. This was shown not to be true by an additional ANOVA of daily suppression ratios in Groups 4-2 and 2-2 of Experiment I and Groups 4-2 and 4-4 of Experiment II. This analysis showed no effect of time difference ($F_{1/28} = 3.74$, $P > 0.05$), but significant effects of groups ($F_{1/28} = 6.94$, $P < 0.05$), days ($F_{6/168} = 12.26$, $P < 0.001$) and the time versus groups interaction ($F_{1/28} = 4.51$, $P < 0.05$). These results indicate that defensive conditioning was more effective when the same numbers of defensive and alimentary trials were presented in one session (Groups 2-2 and 4-4), and less effective when there were

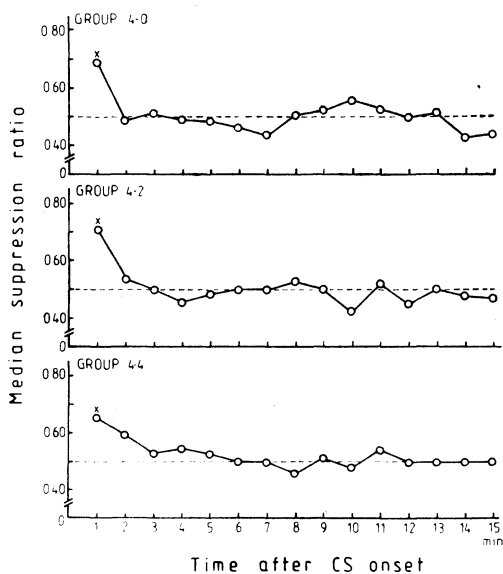


Fig. 3. Median enhancement ratios calculated for fifteen consecutive minutes after the onset of the prolonged CS_{alim} during the first extinction session. The numbers of barpresses emitted during the last minute before the CS onset were used as A to calculate the B/(A + B) ratio for each minute of CS_{alim} independently. Denotations as in Fig. 2.

more CS_{alim} than CS_{def} presentations (Groups 4-2). Moreover, the exceptional effectiveness of defensive conditioning in Group 2-2 of Experiment I was related to the small number of both alimentary and defensive trials rather than to time difference from the seasonal change. As far as daily enhancement ratios obtained during CS_{alim} presentations are concerned, similar ANOVA showed that neither seasonal change, group effects nor their interaction were significant. This indicates that alimentary conditioning was equally effective regardless of whether only alimentary or both alimentary and defensive trials, balanced or unbalanced in numbers, were used during training.

Extinction of the conditioned enhancement. The method of extinction employed for all groups of Experiment II consisted in an extreme prolongation of the CS_{alim} action with simultaneous withdrawal of the CRF. This provided an opportunity to test persistence of behavior previously conditioned to that CS. As seen from Fig. 3 showing results from the first extinction day, conditioned enhancement was observed only during the first minute of CS_{alim} action, and then the $B/(A + B)$ ratios fluctuated around 0.5. The A-B comparisons based on numbers of barpresses emitted one minute before and one minute after CS_{alim} onset showed that in Group 4-0 significant enhancement was observed during the 1st-4th, 6th and 10th extinction sessions, in Group 4-2 during the 1st-6th and 10th extinction session, and in Group 4-4 during the 1st, 2nd and 4th extinction sessions ($P < 0.05$ or better, Wilcoxon matched-pairs two-tailed tests). Similar A-B comparisons for numbers of barpresses emitted one minute before the CS_{alim} onset and during the second minute of its prolonged action showed significant enhancement only in one case: in Group 4-0 during the 2nd extinction session. In no case was significant enhancement observed during the third minute of the prolonged CS_{alim} action.

The above analyses suggest that resistance of the CS_{alim} to extinction was the lowest in Group 4-4 of Experiment II. However, this inference has to be taken with caution. A weakness of the above analyses is the short periods of time, only one minute each, used for the A-B comparisons of barpressing rates. Some fluctuations of the base-line barpressing rate have been commonly observed even in well trained rats. To reduce the consequences of such fluctuations, it was decided to compare numbers of barpresses emitted during the ten consecutive minutes before with those during the three consecutive minutes after the onset of the prolonged CS_{alim} . The statistical test developed for such comparisons and the results obtained are presented in separate paper in this issue (23). Generally, these additional analyses confirmed the resistance of enhancement of barpressing after the onset of the CS_{alim} in all Groups of Experiment II and the rapid decline of the rate of barpresses with the passage of time during the prolonged action of this stimulus.

Baseline responding. To account for changes in baseline responding, rates of barpresses emitted during the A periods of the *P*-days and the 1st-7th days of acquisition training were analyzed for each experiment independently. For the last day of the preliminary training (*D*-day) prior to the *P*1-day the numbers of barpresses

in 1 min intervals corresponding to the pre-CS periods in next sessions were collected and also included in the analyses. For Experiment I the ANOVA showed no group effect, but significant effect of days ($F_{8/224} = 2.11, P < 0.05$) and an interaction of groups and days ($F_{24/224} = 2.11, P < 0.01$). With data collapsed across groups the lowest barpressing rate was observed during the *D*-day and further Duncan tests showed that the rates of responding on *P2*-day and the 1st, 2nd, 5th, 6th, and 7th days of conditioning were higher ($P_s < 0.05$). The significant group versus day interaction was due to the fact that, in contrast to Group 4-0 and Group 0-0, the lowest barpressing rate in Group 4-2 was observed during the 3rd day, and in Group 2-2 during the 4th conditioning day. Thus, a monotonic increase of on-going barpressing in Group 4-0, in which only CS_{alim} was presented, and in Group 0-0 serving as a control without CSi presentations, was contrasted with an initial decrease and subsequent increase of barpressing rate in Groups 4-2 and 2-2, which had both CS_{alim} and CS_{def} presented. A similar but less regular picture was observed in Experiment II where an ANOVA showed no group effect, but significant effects of days ($F_{9/189} = 3.23, P < 0.01$) and groups versus days interaction ($F_{18/189} = 1.82, P < 0.05$).

Comparison of barpressing rates before and after the trial may give some information about the immediate effect of the CS on baseline responding. These data for each experimental group of the Experiments I and II are presented in Fig. 4. To determine the post-effects of the CS_{alim} presentations, the A and C scores for Groups 4-0 of both experiments during the 1st-7th acquisition sessions were com-

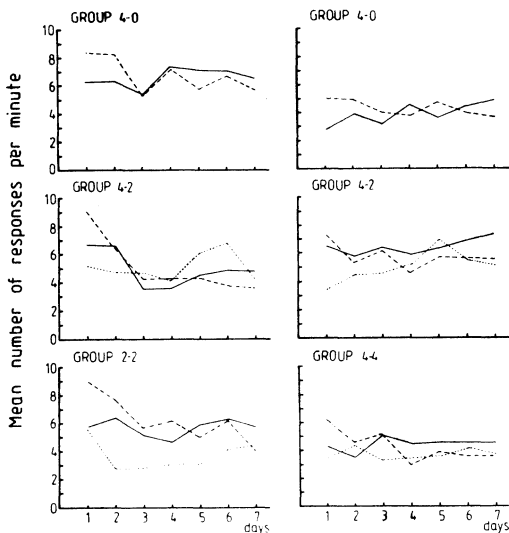


Fig. 4. Mean numbers of barpresses per min emitted during one min periods before (solid lines) and after CS_{alim} (broken lines) or after CS_{def} (dotted lines) in each experimental group of Experiments I (left panel) and II (right panel) for each of the 1st-7th conditioning sessions.

pared. An ANOVA showed an effect of group ($F_{1/14} = 13.63$, $P < 0.005$), no effects of days nor scores, and significant interaction of days with scores ($P_{6/84} = 5.52$, $P < 0.001$). Examination of the data indicated that at the beginning of conditioning, A scores were lower than the C scores, whereas at the end of training the opposite was found. This change in relation between the A and C scores occurred earlier in Group 4-0 of Experiment I, which was characterized by high barpressing rates, than in Group 4-0 of Experiment II. Generally, barpressing rates were higher in Experiment I than in Experiment II.

For groups in which both conditioned enhancement and conditioned suppression were trained, three different scores were compared: A scores, C scores after CS_{alim} and C scores after CS_{def} . An ANOVA based on data from Group 4-2 and Group 2-2 of Experiment I and from Group 4-2 and Group 4-4 of Experiment II showed no group effect, but did show an effect of days ($F_{6/160} = 5.44$, $P < 0.001$) and effect of scores ($F_{2/56} = 8.13$, $P < 0.001$). Moreover, several interactions were significant: groups with scores ($F_{6/56} = 2.46$, $P < 0.05$), days with scores ($F_{12/336} = 9.34$, $P < 0.001$) and the interaction of the three main effects ($F_{36/336} = 2.12$, $P < 0.005$). Inspection of the data indicated that the highest level of responding was before the trials and the lowest was after CS_{def} . Especially low barpressing rate after CS_{def} were observed in Group 2-2 of Experiment I and Group 4-4 of Experiment II. The overall level of responding was highest at the very beginning of conditioning and lowest during the 4th session of conditioning. This decrease was due

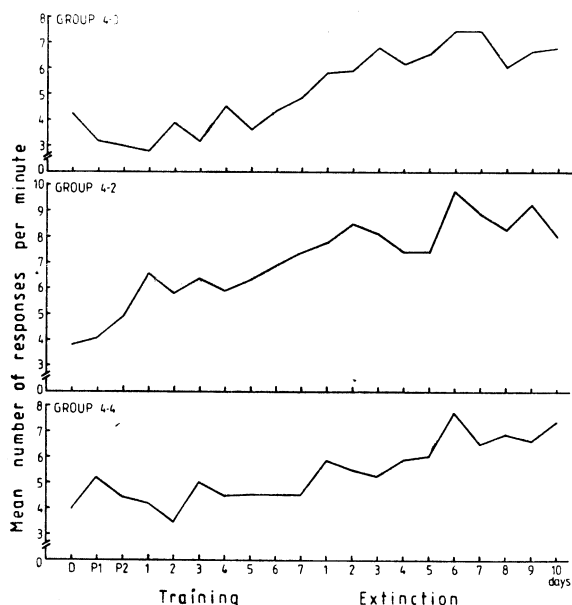


Fig. 5. Mean numbers of barpresses per min emitted in pre-CS periods during all consecutive stages of Experiment II for each Group independently.

to a marked drop in responding after CS_{alim} presentations, whereas changes in rates of barpresses during A periods and after CS_{def} presentations were smaller, and some initial decline in responding was followed by full recovery.

As seen from Fig. 5, a steady increase in the number of barpresses in the A periods was observed in all groups of Experiment II not only during conditioning training, but also during the extinction sessions. An ANOVA based on the numbers of barpresses emitted in A periods during the last sessions of preliminary training (*D*-day), two *P*-days and seven sessions of conditioning all considered as one stage, and similarly the ten sessions of extinction constituting the second stage, showed a very pronounced effect of stages ($F_{1/21} = 79.58$, $P < 0.001$), and significant interaction of the three main effects ($F_{18/189} = 2.19$, $P < 0.05$), but no group effect. The triple interaction was presumably due to Group 4-4, which did not show a rise of barpressing rate during the conditioning training stage.

The increase of barpressing rate had very little effect on the number of food pellets received by rats. We were able to retrace in four rats from each group of Experiment II the exact numbers of food pellets received during consecutive sessions of training. Table II presents the mean rates of barpressing in three consecutive

TABLE II

Mean numbers of barpresses per min and mean numbers of food pellets received per 2.5 min at different stages of the experiment. Data obtained on four rats sampled from each group of Experiment II

Stage of experiment	Group 4-0	Group 4-2	Group 4-4
Barpressing rate			
Preliminary training	3.2	2.8	3.0
Conditioning training	2.6	5.0	3.8
Extinction	5.0	6.3	5.1
Food pellets received per 2.5 min			
Preliminary training	0.94	0.96	0.97
Conditioning training	0.97	1.11	1.08
Extinction	1.00	0.98	1.03

stages of the experiment and the numbers of food pellets received per 2.5 min periods. For the acquisition stage of the experiment, the responses emitted, pellets received, and time occupied by presentations of the CS_{alim} signaling the CRF schedule were excluded from calculations. As indicated in the Table, the barpressing rates increased in each group about twice in the course of the experiment. However, the mean numbers of food pellets received per 2.5 min periods changed very little. The minimal interval between two opportunities to receive food pellet in this 2.5 min VI schedule of reinforcement was 6 s. The number of pellets received by a rat

performing barpresses every 6 s very regularly would be 1.00. Even during the preliminary training this index was not lower than 0.94. Indices higher than 1.0 were due to the procedure used, since the first barpress at the beginning of each session was reinforced by a pellet and in many instances the same was true after the 1 min periods in which CS_{alim} and CRF were given. This second distortion of the index cannot be easily corrected.

The data collected on the four rats from each group showed additionally that rats differed in their ability to use the CRF schedule signaled during the acquisition stage by the CS_{alim} . The worse learners received about 30 and the best learners more than 50 percent of all food pellets during the 120 min session as a reinforcement of barpresses emitted during the four 1-min presentations of the CS_{alim} . The ability to use the CRF schedule was learned very rapidly, during one and no more than two sessions, and then the percentages of pellets received by a given rat during the CS_{alim} showed only minimal fluctuations. Good and poor learners were observed in each group and this ability was not correlated with the level of barpressing rate typical for a given rat.

DISCUSSION

The present study indicates that rats easily acquired conditioned enhancement of barpressing as a result of the change of the 2.5 min VI schedule of food reinforcement to a multiple schedule: 2.5 min VI, CRF. In our experiments the second component of the multiple schedule was signalized by darkness. When the 2.5 min VI schedule was again resumed for the entire session, the onset of darkness retained its property to enhance on-going barpressing behavior. Data presented in this and in the related paper (23) indicate that conditioned enhancement was weakened but not removed in the course of ten extinction days, each consisting in a one hour presentation of darkness without the CRF schedule during a total session duration of 2 h.

Several factors may contribute to small effectiveness of the extinction procedure used in Experiment II of this study. As it was reported by Konorski (17), extinction of the alimentary CS presented against the alimentary background is handicapped. Moreover, the 2.5 min VI food reinforcement schedule was in effect during prolonged action of the stimulus subjected to extinction. The acute extinction procedure has also a discriminative component. Since during acquisition stage of the experiments stimuli of only 1 min duration were used, a long lasting stimulus was clearly different and thus would not contribute much to extinction of the short one. Effects of other extinction procedures will be presented in next papers.

In some of the experimental groups during the 2.5 min VI component of the multiple schedule, the CS_{def} , an acoustic stimulus terminating with inescapable shock, was presented. This resulted in acquisition of conditioned suppression simultaneously with the conditioned enhancement training. Acquisition of the condi-

tioned enhancement was equally effective irrespective of the numbers of defensive trials applied during the training sessions. Between-group differences in numbers of trials in which conditioned enhancement was observed and also in resistance of this behavior to extinction seem to be unsystematic. On the other hand, defensive conditioning was more effective when the same numbers of CS_{def} and CS_{alim} were presented and less effective when there were more CS_{alim} than CS_{def} presentations. The most effective defensive conditioning was observed in Group 2-2 of Experiment I, in which small numbers of both alimentary and defensive trials were presented during acquisition sessions. All of these findings indicate that conditioned enhancement training has some negative effect on the acquisition of the conditioned suppression.

Several different mechanisms may be proposed to account for the attenuating effect of conditioned enhancement on conditioned suppression. An explanation focused on stimulus generalization between CS_{alim} and CS_{def} has to be discarded because the two stimuli, darkness and acoustic white noise, were of different modalities, they never overlapped in time, and signaled opposite biologically important events: the possibility of obtaining food pellet for each barpress versus inescapable shock. Even in the situation, when the same event, an inescapable shock, has been signaled by stimuli of different modalities, no transfer of suppression from one CS to the other stimuli occurred (24, 27). The mechanism suggested by Stein, Sidman and Brady (20), by which the amount of conditioned suppression is inversely related to the proportion of time occupied by the CS_{def} in the experimental session, has no relevance to our experiments. In fact, acquisition of conditioned suppression was retarded only when the number of CS_{def} was smaller than the number of CS_{alim} presentations. One may say that a few defensive trials become overshadowed by the more numerous trials with continuous food reinforcement.

There are several observations indicating that the rate of learning the conditioned suppression, its final level and resistance to extinction all depend on the schedules of appetitive reinforcement used to maintain the on-going behavior. Generally, conditioned suppression is more pronounced when relatively low frequencies of food or water reinforcements are permitted by the schedule (18). Trial-to-trial variability of suppression ratios is much smaller under VI schedules of reinforcement that produce a steady rate of responding than under other schedules characterized by bimodal distributions of inter-response times (19-21). In the context of the present study it is worthwhile to mention early experiments by Brady, who showed low resistance of conditioned suppression to extinction when rats were transferred to continuous reinforcement or to fixed ratio schedules after training under a VI schedule (5, 6). In an attempt to exploit this attenuating effect of the CRF schedule on conditioned suppression, Hoffman introduced a method of differentiation learning in which CS^+ signaled inescapable shock and produced suppression, whereas some parts of the CS^- presentations were accompanied by CRF for pecking a key (14, p. 207-211). The increase of the reinforcement density provi-

ded by the CRF schedule did not prevent generalization of suppression from the CS⁺ to the CS⁻ but evidently retarded acquisition of conditioned suppression. The learning function obtained under these conditions by Hoffman was very irregular and similar to those showed in Fig. 2 by Group 4-2 of both experiments. Hoffman's data suggested that it is not conditioned enhancement but the introduction of the CRF schedule that affects acquisition of the conditioned suppression.

If this interpretation of Hoffman's data is correct, they give support for central inhibitory influence of excitatory stimuli on responding maintained by stimuli signaling opposite motivational state. The present study also supports such view. Dickinson and Pearce (9) in their theoretical paper reviewed most of the experimental data concerning inhibitory interactions between appetitive and aversive stimuli according to three behavioral criteria: the summation, retardation and counterconditioning tests. Summation criterion seems appropriate for consideration of the changes in the on-going barpressing rate during intertrial intervals in Alimentary-Defensive Groups.

The CRF component of the multiple schedule had two easily observed effects. At the beginning of training enhanced barpressing was observed not only during the CS_{alim} but also continued after the termination of this stimulus. Such post-CS_{alim} enhancement disappeared with further training. The second effect of the CRF was the general increase of baseline responding evidenced by the monotonic increase of the numbers of barpresses during the pre-CS periods (11). These effects are just opposite to those elicited by a CS signaling inescapable shock. At the beginning of conditioned suppression training the termination of the CS_{def} produced slowing of barpressing. This effect gradually disappeared in the course of training. The second effect, a general decrease of response rate reflected in smaller numbers of barpresses during pre-CS periods, was longlasting and followed by a gradual but not complete recovery of barpressing rate (15, 30, 31, 33-36). In the present experiments both these effects of the introduction of the CS_{def} and shock were markedly attenuated and restricted to only a few training sessions in the groups in which not only conditioned suppression but also conditioned enhancement had been trained.

The final conclusion by Dickinson and Pearce (9) was that inhibitory influences of appetitive stimuli on aversively motivated behavior are less documented than influences of aversive stimuli on appetitive behavior. Our data indicate the bidirectional influences between aversive and appetitive stimuli, but generally showed the predominance of alimentary over defensive influence on the on-going behavior. One reason for such effect is high level of alimentary motivation in hungry rats and opportunity to obtain food in each moment of the experimental session. However, the index used in this study may also contribute to the results. Instead of observing behavioral consequences of combined-cue presentations, the attention was focussed on changes in the on-going responding related to longlasting effects of the CS_{def} and CS_{alim} and their interactions. This gives an opportunity to over-

come some of weaknesses of regular summation tests, such as changes in attentional value of stimuli during their simultaneous presentation and competition between incompatible peripheral responses.

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