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STIMULUS MODALITY EFFECTS ON TRANSFORMATIONS OF CONDITIONED ENHANCEMENT AND CONDITIONED SUPPRESSION IN RATS

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Abstract. Unconditioned and conditioned effects of house-light offset and acoustic white noise on barpressing behavior maintained by intermittent food reinforcement were tested in male hooded rats. Presentations of these stimuli prior to their acquiring signal value initially tended to depress and then to enhance barpressing rate, but generally the rate of the on-going barpressing was lower during the light offset then during noise presentations. Subsequently, one stimulus was used to signal continuous food reinforcement, evoking conditioned enhancement, and the other to signal inescapable footshock eliciting conditioned suppression of barpressing. The enhancement was acquired more rapidly than the suppression, independent of the stimulus modality used. The stimulus modality effect emerged when the continuous food reinforcement was withdrawn, since enhancement elicited by light offset extinguished more rapidly than elicited by noise. The stimulus modality effect was stronger when the other stimulus continued to signal pain and was attenuated when conditioned suppression was also extinguished. During the next stage of the experiment, the signal values of the conditioned stimuli were reversed, resulting in easy transformation of conditioned suppression into conditioned enhancement and vice versa. The stimu-

li used and changes in their signal values exerted clear effects on the rate of barpressing during intertrial intervals and this, in turn, somewhat modulated the behavioral effects of the conditioned stimuli. These results indicate that unconditioned effects of the stimuli on the behavior interact with their properties acquired in the course of conditioning.

INTRODUCTION

Recently, it has been shown (24) that rats easily acquired conditioned enhancement of barpressing as a result of the change from a 2.5 min variable interval (VI) schedule of food reinforcement to a multiple schedule in which the second component, continuous food reinforcement (CRF), was signalled by an external stimulus, i.e. darkness (house light offset). The resulting multiple schedule, 2.5 VI, CRF, was presented for 2 h daily and, to prevent satiation, the CRF component was given only several times within a session, each time for one min. Under these conditions, an external stimulus signalling CRF may be considered as a sporadic conditioned alimentary stimulus (CS_{alim}). Some groups of rats were trained in a more complex situation, in which during the 2.5 min VI component of the multiple schedule, a conditioned defensive stimulus (CS_{def}) of another modality terminating with inescapable shock was presented (24). After brief training, the CS_{def} elicited conditioned suppression of the on-going barpressing (9).

Parallel training in conditioned enhancement and conditioned suppression makes it possible to investigate interactions between alimentary and defensive modes of responding, and how different experimental variables affect these interactions. Generally, alimentary and defensive modes of behavior are accepted as antagonistic, and inhibitory interactions exist between stimuli evoking these behaviors, which may be investigated using different tests. According to Dickinson and Pearce (7), these tests may be classified into three categories: (i) a summation or combined-cue test, (ii) retardation or resistance-to-reinforcement procedure, and (iii) counterconditioning.

Training of conditioned suppression is the most commonly used procedure for testing the effects of summation of the apparatus cues evoking baseline appetitive responding with the CS_{def}. Most researchers have focused attention on a drop in responding during the CS_{def} action, however, an over-all decrease in on-going appetitive responding during intertrial intervals has been observed in many studies (1, 6, 12, 21, 24, 27, 29, 30, 33) indicating a more general influence of the defensive on the appetitive mode of responding. The opposite effect of appetitive on defensive behavior may be illustrated by the strong dependence of suppression

magnitude on the schedule of reinforcement used to maintain the ongoing appetitive behavior (3, 19). The complexity of these interactions may be further documented by data showing that the CRF and/or conditioned enhancement exert a decremental effect on conditioned suppression, but only when defensive trials are less frequent than trials with CRF of barpresses (24).

The summation test gives an opportunity to investigate interactions between actual values of stimuli, either acquired or inborn. Let us limit our consideration to inhibitory interactions between stimuli signalling values of which were acquired in the process of conditioning. With this limitation, the other two categories of tests mentioned by Dickinson and Pearce (7) concern interactions occurring in the process of transformation of the already acquired associations. Konorski (16) distinguished between homogenic and heterogenic transformations. The former consists in the withdrawal of the unconditioned stimulus (US), which had previously followed the CS presentations, or in the introduction of the US to the CS previously presented alone. Heterogenic transformation consists in the change of a specific US for the antagonistic US, i.e., a CS regularly followed by food is then followed by shock to the paw or vice versa. Independent of whether homo- or heterogenic transformations are involved, the retardation test is employed, when attention is focused on the number of CS—US pairings necessary for the CS to acquire new signalling properties. Alternatively, if attention is concentrated on changes in the response pattern initially elicited by the CS, the procedure is considered as counterconditioning (7). Within the last category, Konorski distinguished a special case of transformation of association, when another, antagonistic reaction, is required to secure satisfaction of a given drive, which he labelled as reversal learning of instrumental responses (16). In traditional Pavlovian terminology, the procedure in which a pair of stimuli interchange their signalling values is termed reversal learning independent of whether homo- or heterogenic transformations are involved, classical or instrumental responses are used, and attention is focused on rapidity of the learning or on changes in response patterns.

All of these considerations indicate an inconsistency of existing classifications of procedures used for the investigation of inhibitory interactions between stimuli having different signalling values. Neither Dickinson's nor Konorski's classifications of categories are exclusive. At least partial extinction of previously acquired associations have to be involved in all instances of transformations. Thus, until satisfactory classifications of tests are developed, we will narrow our interests to investigate resistance-to-change of the acquired alimentary and defensive associations using extinction and reversal learning procedures.

The complexity of interactions between alimentary and defensive stimuli suggests that results obtained in any testing procedure may depend on many experimental variables, one of which is the modality of conditioned stimuli. Perspective CSi differ in their affinity to appetitive and aversive USi (10), thus some CSi would facilitate and others retard the learning process. Moreover, the saliency of stimuli used as CS_{alim} and CS_{def} may influence the interrelations between them tested by any procedure. In effect, some of the controversial results concerning inhibitory interactions between appetitive and aversive stimuli (7) may be due to qualitative and quantitative characteristics of the CSi used.

Specifically, in our first report a decremental effect of the CRF and/or conditioned enhancement on conditioned suppression was noted (24). This result, suggesting a predominance of alimentary over defensive behavior was obtained with darkness used as CS_{alim} and acoustic white noise as CS_{def}. On the other hand, in the next study it was shown that the transformation of conditioned suppression to conditioned enhancement was less effective than the simultaneously conduced transformation of conditioned enhancement into conditioned suppression (25). In the latter experiment acoustic white noise was used as the CS_{alim} and darkness as the CS_{def} for original training of conditioned enhancement and conditioned suppression. Comparison of these two sets of data may suggest that inhibitory interactions between appetitive and aversive conditioned stimuli are influenced by their modalities.

In the present study, different indices were analysed to test the nonequivalence of darkness and acoustic white noise stimuli on acquisition, extinction and reversal learning of conditioned enhancement and conditioned suppression. Part of the data from two groups of rats (denoted in the present paper as Group 2 and Group 4) has been presented previously in Russian (26).

MATERIAL AND METHODS

Each of the four experimental groups consisted of 8 naive male hooded rats, all from the same colony and approximately 3 months old at the start of the experiment. 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 experiment, all rats were reduced to 75% of their free-feeding body weight and were maintained at that weight throughout the

investigation. During the experiment a 22 h schedule of food deprivation was applied, and daily ration of food was given just after each experimental session. The preliminary training consisted of initial presentation of 40 "free" 45 mg food pellets on a 1 min variable interval (VI) schedule of reinforcement, 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. 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.

The last day of the preliminary training constitutes so called Dummy Day (D Day) in which no stimuli were presented but numbers of barpresses were collected and analysed similarly as in the following sessions.

The preliminary training was followed by two Pretest Days (P1 and P2), during which to-be-conditioned stimuli (70 dB white noise or darkness) were presented alone at appropriate times in the session for 1 min periods. The next stage consisted of seven days of conditioning training. During this stage of experiment, alimentary conditioned stimuli (CS_{alim}) were given four times and defensive conditioned stimuli (CS_{def}) twice at appropriate times, in changing sequence decribed previously (24), during each 2 h session. In Group 1 and Group 2 the CS_{alim} was 1 min of darkness and the CS_{def} was 1 min of 70 dB (re: 20 $\mu N/m^2$) acoustic white noise. In Group 3 and Group 4 the CS_{alim} was 1 min of 70 dB white noise and the CS_{def} was 1 min of darkness. During the action of CS_{alim} each barpress was reinforced by a food pellet, and the CS_{def} terminated with 1 s of inescapable scrambled footshock of 2 mA intensity.

The next stage consisted of 10 days of extinction of the conditioned enhancement. The CS_{alim} was presented as before but during its 1 min action the CRF of barpresses was withdrawn and only 2.5 min VI schedule was effective, similar to the reinforcement density of the intertrial intervals. In Group 1 and Group 3 extinction of the conditioned suppression was conducted in parallel. For these two groups the CS_{def} was presented without shock during the extinction stage. In Group 2 and Group 4, on the contrary, training of conditioned suppression was prolonged and during the extinction of conditioned enhancement, the CS_{def} terminated with aversive shock as before.

The last stage of the experiment was reversal learning. During 10 daily sessions the signalling properties of the conditioned stimuli were reversed. Thus, in Group 1 and Group 2 darkness terminated with shock

(CS_{alim} changed to CS'_{def}) and 70 dB noise signalled CRF (CS_{def} changed to CS'_{alim}). Similarly in Group 3 and Group 4, noise was the CS'_{alim}. The original and reversed meanings of the conditioned stimuli are shown in Table I.

TABLE I

Signalling values of darkness (D) and acoustical white noise (N) in consecutive stages of experiment for each group. CS_{alim} denotes the conditioned stimulus signalling CRF, CS_{def} indicates the conditioned stimulus paired with inescapable shock, CS_{ext} denotes conditioned stimulus what had the previously signalled value subjected to extinction, CS'_{alim} and CS'_{def} denote conditioned stimuli acquiring their new signalling values in the course of reversal learning

Stage	Acquisition	Extinction	Reversal
Group 1	D—CS_{alim} N—CS_{def}	D—CS_{ext} N—CS_{ext}	D—CS'_{def} N—CS'_{alim}
Group 2	D—CS_{alim} N—CS_{def}	D—CS_{ext} N—CS_{def}	D—CS'_{def} N—CS'_{alim}
Group 3	N—CS_{alim} D—CS_{def}	N—CS_{ext} D—CS_{ext}	N—CS'_{def} D—CS'_{alim}
Group 4	N—CS_{alim} D—CS_{def}	N—CS_{ext} D—CS_{def}	N—CS'_{def} D—CS'_{alim}

The numbers of barpresses emitted by each rat were collected for each 30 s period. A,B, and C denote numbers of barpresses emitted in 1 min periods immediately before CS onset, during the CS action, and immediately after CS termination, respectively. The magnitude of changes in the barpressing rate during CS_{alim} and CS_{def} presentations was measured by computing the B/(A + B) ratio described by Annau and Kamin (1). Daily ratios were computed for each rat by summing responses emitted during the appropriate intervals of a given kind of trial.

The B/(A + B) ratio was introduced with assumption that the more fear to the CS, the larger percentage of the on-going appetitive behavior was suppressed (1). With this assumption correct, the ratio eliminates influence of baseline responding fluctuations, either between or within subjects, on the measure of the conditioned defensive response strength. The distribution of the ratio is, however, not symmetrical in respect to the no-change value of 0.5. The same percentage change of the on-going behavior exerts greater effect on the suppression than on the enhancement B/(A + B) ratio. In consequence, the graphs construced on the B/(A + B) ratios suggest stronger effect of the CS_{def} than of the CS_{alim}. Since in this paper conditioned suppression and conditioned enhancement

were simultaneously tested, it was decided to present in Figures the mean numbers of responses per minute. However, to eliminate daily fluctuations of barpressing rate the statistical analyses were based on the suppression/enhancement ratios of B/(A + B).

RESULTS

Pretest days

Presentations of the 70 dB white noise and the offset of a house light, each without any consequence, provided information about unconditioned effects of the to-be-conditioned stimuli on the on-going barpressing rate. These effects were rather weak. The A-B comparisons done for each stimulus presentation and group of rats independently showed that darkness elicited significant suppression of barpresses in 12.5% of cases, whereas the noise evoked suppression in 8% of cases and produced enhancement of barpresses in 4% of cases. Significant suppression of barpresses was observed mostly during early presentations and especially to the modality less frequently presented for a given group of rats. All

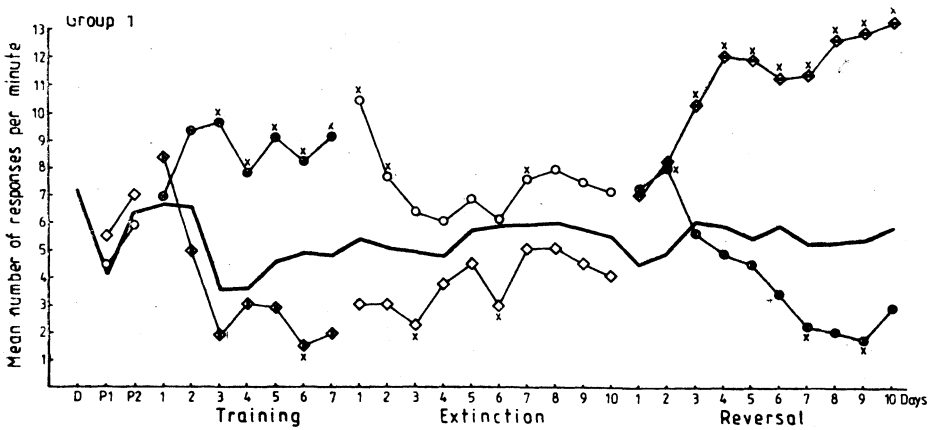

Fig. 1. Mean numbers of barpresses per min emitted in one min periods before and during the action of the CSi on consecutive days of the experiment for Group 1. The line without symbols denotes the on-going responding rate and lines with symbols denote rates of responding during presentations of stimuli. Diamonds indicate the 70 dB white noise CS and circles show the darkness CS. Open symbols denote CSi presented without any other change in the experimental situation. Symbols with a horizontal bar indicate CSi signalling continuous food reinforcement for barpresses. Symbols with a vertical bar are used for CSi presented with the shock US. Crosses below or above the symbols for daily ratios signify suppression or enhancement levels that were respectively significant at $P < 0.05$ or better, as estimated by A-B comparisons (Wilcoxon test).

instances of significant unconditioned suppression were observed in Group 2 and Group 3.

These statistical evaluations underestimate differences between unconditioned effects elicited by the two stimuli. Data presented in Figures 1-4 clearly indicate that the typical effect of the noise presentation was

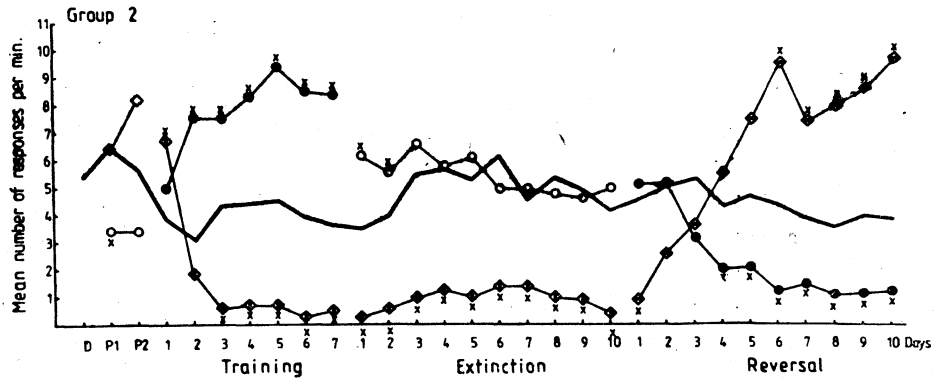

Fig. 2. Mean numbers of barpresses per min emitted in one min periods before and during the action of the CSi on consecutive days of the experiment for Group 2. Other denotations as in Fig. 1.

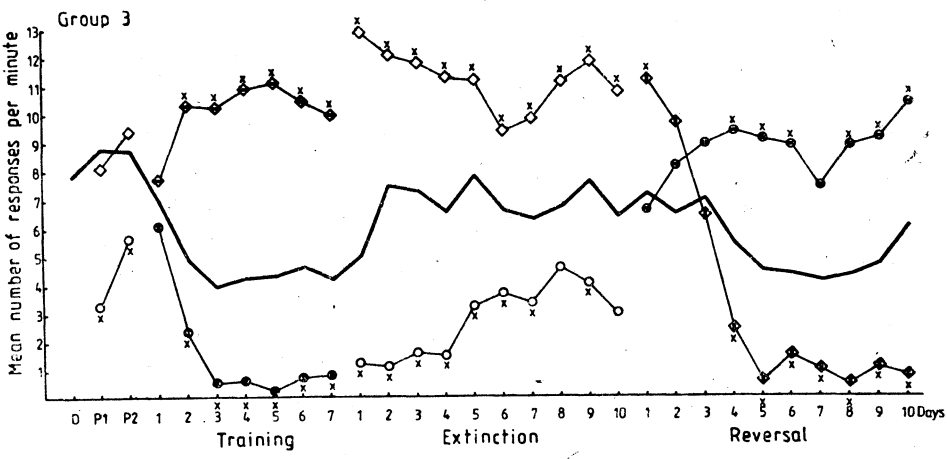

Fig. 3. Mean numbers of barpresses per min emitted in one min periods before and during the action of the CSi on consecutive days of the experiment for Group 3. Other denotations as in Fig. 1.

an acceleration, whereas that of the darkness was a slowing down barpressing rate. Thus our inference about differences between unconditioned effects of the two stimuli ought perhaps to be based on comparisons of the barpressing rate during presentations of these stimuli (B for noise,

B for darkness comparisons) instead of the A-B comparisons for each stimulus independently presented above. Such B-B comparisons based on daily rates of responding within a given Pretest day and group showed that in each case the rate of responding was higher during the noise

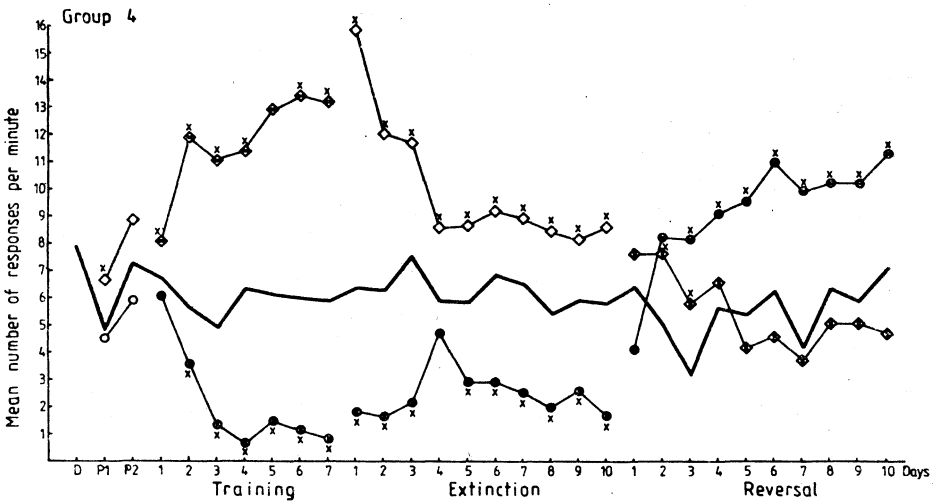

Fig. 4. Mean numbers of barpresses per min emitted in one min periods before and during the action of the CSi on consecutive days of the experiment for Group 4. Other denotations as in Fig. 1.

than during the darkness presentations. Except for Group 1 all such comparisons were significant at the $P < 0.01$ or $P < 0.02$ levels (Wilcoxon test, two-tailed).

Acquisition of the conditioned enhancement and coniditioned suppression

The effects of contingencies employed during consecutive days and stages of the experiment are presented in Figures 1-4 by the mean numbers of responses emitted during the A periods (baseline responding) and during the B periods for CS_{alim} and CS_{def} independently. As confirmed by a $2 \times 2 \times 7$ ANOVA based on the B/(A + B) ratios, neither the modality of simuli, nor groups had any effect on conditioned enhancement during the acquisition stage of the experiment, whereas the main effect of days ($F_{6/168} = 12.26$, $P < 0.001$) and days with groups interaction ($F_{6/168} = 5.17$, $P < 0.001$) effects were significant. The introduction of the CRF schedule during CS_{alim} presentations was very effective. Daily data indicate that during the first day of training 75% of the rats reacted to the CS_{alim} by enhancing barpressing and for the second day of training

this index was 94%. During the 2nd-7th days of training, the CS_{alim} did not elicit conditioned enhancement only in 3% of the cases, mostly in the Group 1, which was responsible for days vs groups interaction mentioned above.

A similar analysis of the daily data for CS_{def} indicated that training of conditioned suppression was slower and less effective. During the first day of training only 47% of the rats reacted by suppressing responses during the CS_{def}, and for the second day of training this index was 78%. It must be stressed that during the second day of training, the CS_{def} did not elicit suppression in three rats from Group 1, in three rats from Group 2 (both trained with noise CS_{def}) and in one rat from Group 3 (trained with the darkness CS_{def}). During the 3rd-7th days of training the white noise CS_{def} did not evoke suppression in 11 cases (10 times in Group 1), whereas the darkness CS_{def} elicited suppression in each case. All of these group differences were supported by an ANOVA based on daily B/(A + B) ratios for CS_{def}, which showed an effect of stimuli ($F_{1/28} = 8.38$, $P < 0.01$), interaction of stimuli with groups ($F_{1/28} = 7.84$, $P < 0.01$), an effect of days ($F_{6/168} = 32.83$, $P < 0.001$) and interaction of the three main factors ($F_{6/168} = 2.50$, $P < 0.05$). The overall suppression ratios were the lowest (i.e., greatest response suppression) in Group 3 and the highest (i.e., smallest suppression) in Group 1.

Additional analyses showed that by the 5th day of training, the B/A + B) ratios reached asymptote for both conditioned enhancement and conditioned suppression and did not change significantly in next days of training for each group. Inspection of Figures 1-4 supports this conclusion.

Extinction

As seen from Figures 1-4, during the extinction of conditioned enhancement a clear-cut modality effect was observed. Withdrawal of the CRF during the CS_{alim} resulted in substantial attenuation of the conditioned enhancement to the darkness CS_{alim} (Group 1 and Group 2), whereas changes observed during extinction of the noise CS_{alim} (Group 3 and Group 4) were small and unsystematic. An $2 \times 2 \times 10$ ANOVA based on daily B/(A + B) ratios for CS_{alim} under extinction showed significant effects of stimuli ($F_{1/28} = 9.60$, $P < 0.005$) and days ($F_{9/252} = 5.35$, $P < 0.001$), whereas effect of groups and all interactions were far from acceptable levels of significance. Withdrawal of the CRF during the CS_{alim} was effective for reduction of the magnitude but not for elimination of conditioned enhancement. Comparisons of daily scores for each rat independently showed that during 10 extinction sessions the darkness continued to elicit enhancement in 69% and the noise in 94% of cases.

As outlined above in Methods, extinction of conditioned enhancement was accompanied in Group 1 and Group 3 by simultaneously conducted extinction of conditioned suppression, whereas in Group 2 and Group 4 termination of CS_{def} was coincident with inescapable foot-shock as before. In accordance with differences in training conditions, there were separate analyses completed for results obtained in Groups 1 and 3 and for Groups 2 and 4. These analyses are summarized in Table II and they should be compared with the findings from the same stage of the experiment presented in Figures 1-4. These data indicate that the modality effect on conditioned enhancement subjected to extinction was much more evident in rats continuing defensive training (Groups 2 and 4) than in rats subjected to extinction of conditioned enhancement and conditioned suppression applied in parallel (Groups 1 and 3). Overall mean B/(A + B) ratios presented in Table II indicate that the strongest attenuation of enhancement was observed in Group 2, in which the deepest conditioned suppression to the CS_{def} was maintained. The same data suggest that the procedure employed for extinction of conditioned enhancement was not fully effective. Nevertheless, all analyses and comparisons indicate that enhancing properties of the darkness CS_{alim} were attenuated more than those of the noise CS_{alim}.

TABLE II

Mean B/(A+B) ratios calculated for the entire extinction stage of experiment and values of *F* statistics obtained in four analyses of variance

		CS_{alim} extinction		CS_{def} overtraining	
Group 2		0.540 (darkness)		0.141 (white noise)	
Group 4		0.626 (white noise)		0.245 (darkness)	
Source of variation	*df*	*F*	*P*	*F*	*P*
Stimuli	1,14	5.78	0.029	3.33	0.086
Days	9,126	3.57	< 0.001	1.46	0.169
Interaction	9,126	0.88	ns	0.86	ns
		CS_{alim} extinction		CS_{def} extinction	
Group 1		0.581 (darkness)		0.404 (white noise)	
Group 3		0.640 (white noise)		0.227 (darkness)	
Source of variation	*df*	*F*	*P*	*F*	*P*
Stimuli	1,14	3.82	0.068	4.99	0.040
Days	9,126	2.99	0.003	3.84	< 0.001
Interaction	9,126	1.18	0.313	1.70	0.095

Data for the CS_{def} are not so equivocal. As seen from Table II there was no difference in the amount of suppression between Group 2 and Group 4 in which the CS_{def} was given with the footshock US. Alternatively for Group 1 and Group 3, in which an extinction procedure for CS_{def} was employed, an ANOVA discovered effects from stimulus modality and days. However, it has to be remembered that, in contrast to rather uniform level of conditioned enhancement elicited by the CS_{alim} at the end of the acquisition stage, there were substantial between-group differences observed in B/(A + B) ratios for CS_{def}. As seen from Table III,

TABLE III

Mean B/(A+B) ratios calculated for the 5th, 6th, and 7th days of the acquisition and the 8th, 9th and 10th days of the extinction stages of the experiment for CS_{def} in each group

Group	CS_{def}	Stages Acquisition	Overtraining	Change
Group 2	White noise	0.071	0.127	−0.056
Group 4	Darkness	0.131	0.243	−0.112
		Acquisition	Extinction	
Group 1	White noise	0.308	0.451	−0.143
Group 3	Darkness	0.053	0.340	−0.287

these between-group differences remained basically unchanged, independent of the procedure used during the next stage of experiment, i.e. overtraining of CS_{def} or extinction. A $2 \times 2 \times 3$ ANOVA based on B/(A + B) ratios for CS_{def} in Group 2 and Group 4 calculated for the last three days of training and extinction stages showed no effect of any main factor or their interactions. An identical ANOVA for Group 1 and Group 3 revealed an effect of groups ($F_{1/14} = 7.79$, $P < 0.025$) and stages ($F_{1/14} = 17.83$, $P < 0.001$), whereas sessions effect and interactions were not significant. These findings all suggest that the stimulus modality effect was negligible during either overtraining or extinction of conditioned suppression.

Reversal learning

During this stage of the experiment, previous CS_{alim} was not only presented without CRF but also terminated with aversive footshock, so that it changed to the CS'_{def}. As seen from Figures 1-4, this procedure

was effective in the rapid change of the behavior from conditioned enhancement to conditioned suppression. Daily sessions data showed that during the first day of reversal learning, 72% of the rats reacted with enhancement of barpressing to the CS'_{def}; during the second day, 62%; during the third day, only 41%. This indicates rapid change of the daily B/(A + B) ratios calculated for the CS'_{def} presentations. A $2 \times 2 \times 10$ ANOVA revealed a significant effect of days ($F_{9/252} = 21.41$, $P < 0.001$), a lack of effects of either modality of stimuli or groups, but a significant interaction of the two main effects ($F_{1/28} = 15.39$ $P < 0.001$). The interaction of all three main effects was quite close to acceptable significance ($F_{9/252} = 1.91$, $P = 0.051$). The significant interaction of stimuli and groups was related to low ratios in Group 2 and Group 3, and the 3-way interaction additionally to the lowest initial level of the B/(A + B) ratios in Group 2.

Table IV presents the results of four independent 2×10 ANOVA's based on daily B/(A + B) ratios. These analyses indicate that, similar to the extinction stage, the stimulus modality effect on the transformation of conditioned enhancement to conditioned suppression was very marked in subjects that continued defensive training until reversal learning (Groups 2 and 4). However, the stimulus effect was much smaller in subjects for which reversal learning was applied after procedures for parallel extinction of conditioned enhancement and of conditioned suppression (Groups 1 and 3). Comparison of the group means of the B/(A + B) ratios indicates that the stimulus modality effects were just the opposite in the two situations, resulting in significant interaction of stimuli and group in the $2 \times 2 \times 10$ ANOVA mentioned above.

Concerning the transformation of the conditioned suppression to the conditioned enhancement, a $2 \times 2 \times 10$ ANOVA revealed a significant effect of groups ($F_{1/28} = 5.57$, $P = 0.024$), days ($F_{9/252} = 20.00$, $P < 0.001$), as well as interactions of stimuli with groups ($F_{1/28} = 6.38$, $P = 0.017$), stimuli with days ($F_{9/252} = 2.47$, $P = 0.01$), groups with days ($F_{9/252} = 2.39$, $P = 0.013$) and all three main factors ($F_{9/252} = 4.50$, $P < 0.001$). The group effect reflected the history of training. Due to overtraining of the conditioned suppression, Group 2 and Group 4 started reversal learning with lower levels of the B/(A + B) ratios for CS'_{alim} and in some rats from Group 2 conditioned suppression persisted much longer than in rats from the other groups. The largest increases in values of the B/(A + B) ratios during reversal learning were observed in Group 3 and Group 4 trained with the darkness CS'_{alim}. The lowest values of mean ratios were observed in Group 2 trained with the noise CS'_{alim}, which resul-

ted in the significant 3-way interaction. The results of analyses presented in Table IV are in full agreement with inferences given above.

TABLE IV

Mean B/(A+B) ratios calculated for the entire reversal learning stage of experiment and values of *F* statistics obtained in four analyses of variance

		$CS_{alim} \rightarrow CS'_{def}$		$CS_{def} \rightarrow CS'_{alim}$	
Group 2		0.269 (darkness)		0.473 (white noise)	
Group 4		0.467 (white noise)		0.612 (darkness)	
Source of variation	*df*	*F*	*P*	*F*	*P*
Stimuli	1,14	12.30	0.004	3.82	0.068
Days	9,126	7.39	< 0.001	13.76	< 0.001
Interaction	9,126	0.87	ns	5.02	< 0.001
		$CS_{alim} \rightarrow CS'_{def}$		$CS_{def} \rightarrow CS'_{alim}$	
Group 1		0.395 (darkness)		0.668 (white noise)	
Group 3		0.265 (white noise)		0.605 (darkness)	
Source of variation	*df*	*F*	*P*	*F*	*P*
Stimuli	1,14	4.51	0.05	2.92	0.107
Days	9,126	15.75	< 0.001	6.71	< 0.001
Interaction	9,126	1.72	0.091	0.82	ns

As seen in Figures 1-4 the rapidity of reversal learning was strongly influenced by levels of conditioned enhancement and conditioned suppression prior to the reversal learning. In Groups 1 and 3, in which the procedure of CS_{def} extinction was applied parallel to CS_{alim} extinction, the rate of barpressing to the CS'_{alim} was higher than baseline already by the frist (Group 1) or the second (Group 3) day of reversal learning. Similar rapid change was observed in Group 4, in which large daily fluctuations of overtrained conditioned suppression were observed during extinction. In all of these groups, the transition between barpressing rates for CS'_{alim} and for CS'_{def} were above the on-going barpressing rate either after the first (Group 1 and Group 4) or after the second (Group 3) day of reversal learning. Only in Group 2, marked by nearly complete extinction of the conditioned enhancement and stable, pronounced conditioned suppression, did the rates for CS'_{alim} become higher than the on-going rate later on, beginning at the fourth day of reversal learning. Also only in this group did the transition between barpressing rates for CS'_{alim} and for CS'_{def} occur below the on-going barpressing rate. As seen from Figures 1-4, Group 4 was the only one

in which the comparisons of A and B indices collected for the CS'_{def} did not show significant suppression on any day of reversal learning (Wilcoxon test).

Barpressing rate in intertrial intervals

The on-going barpressing rate is commonly characterized by the A index. The groups did not differ in their overall mean rate of responding during the 1 min periods immediately preceding the conditioned stimuli onsets. However in the course of the experiment, there were observed marked differences in the A index. The highest level of responding was observed during the *D* Day (Group 1 and Group 4) or during the P1 Day (Group 2 and Group 3) and the lowest — during the second day of the acquisition (Group 2), the third day of acquisition (Group 1 and Group 3), or the second day of reversal learning (Group 4). Two 2×30 ANOVA's, one for Groups 2 and 4, the second for Groups 1 and 3, yielded identical results: no effect of groups, an effect of days and an interaction of days with groups, both significant at $P < 0.001$. As seen from Table V,

TABLE V

Mean rates of barpresses in one min periods immediately preceding the CSi onsets (index A). In the first column as a reference the mean number of barpresses per min estimated for all 30 days of experiment are given for each group. In the next columns the rates of responding are given in percentages to the references rate

	Mean rate per min	D, P1, P2 Days	Acquisition	Extinction	Reversal
Group 2	4.53	126.7	85.3	106.8	95.4
Group 4	5.91	111.3	99.2	103.9	93.2
Group 1	5.27	110.2	92.4	100.6	101.3
Group 3	5.91	142.5	77.8	113.0	90.0

in all groups the general pattern of changes of the A index was similar: a marked drop of on-going rate during acquisition, then partial recovery during extinction, followed by a second decrease during reversal learning. During acquisition, the largest decreases of on-going barpressing were observed in Group 3 and Group 2, in which rapid acquisition of conditioned suppression was observed. In these groups, median $B/(A + B)$ suppression ratios were maintained at zero level at the end of the acquisition stage. During reversal learning the largest decreases of barpressing rates were observed in Group 3 and Group 4, in which conditioned suppression was now trained to noise CS'_{def} which, in contrast to the

darkness CS, did not lose its enhancing properties during extinction. Thus, the largest decreases of on-going barpressing was related during the acquisition stage with the most successful defensive learning and during reversal learning — with the most difficult.

The immediate effects of CS and US presentations may be inferred from the comparisons of the response rates before and after each trial. Group means for each consecutive day of acquisition for the A periods and for the C periods after CS_{alim} and after CS_{def} presentations independently are presented in Fig. 5. At the beginning of training in each group

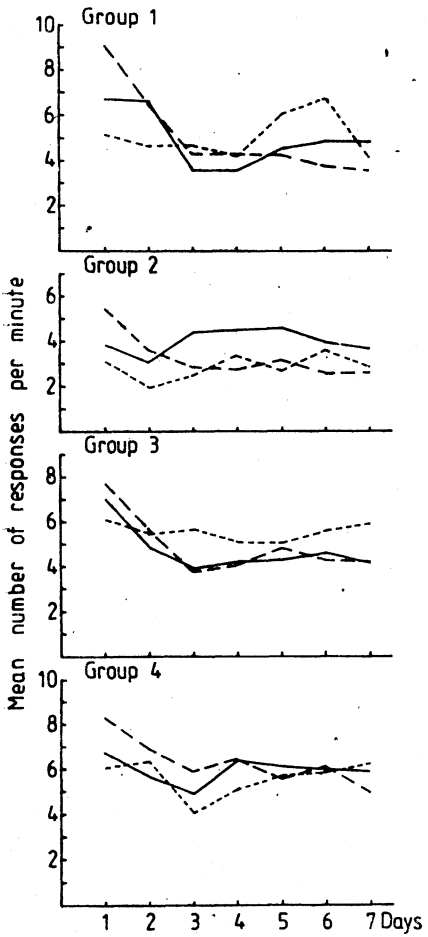

Fig. 5. Mean numbers of barpresses per min emitted during one min periods before (solid lines) and after CS_{alim} (broken lines) or after CS_{def} (dotted lines) in each experimental group for each of the 1st-7th training sessions.

the rate of responding after the CS_{alim} was higher than before the trials and then this difference disappeared or changed to the reverse one. Opposite differences were observed for the CS_{def} presentations.

A 2 × 2 × 7 ANOVA based on numbers of responses emitted in A and C periods for CS_{alim} presentations in Groups 1 and 3 for the seven days of acquisition training yielded an effect of days ($F_{6/84} = 17.42$, $P < 0.001$) only, reflecting the decrease of the barpressing rate mentioned earlier, at the beginning of training. An identical ANOVA done for Groups 2 and 4 showed the effect of groups ($F_{1/14} = 15.14$, $P < 0.005$), days ($F_{6/84} = 2.53$, $P < 0.05$), and days with periods interaction ($F_{6/84} = 9.50$, $P < 0.001$). The effect of groups shown in this analysis reflects the low barpressing rate in Group 2 during training. More interesting is the significant days with periods (A or C) interaction reflecting the gradual decrease of barpressing ratios in C periods during the course of training. Similar ANOVA's were done comparing A and C periods of CS_{def} presentations. An ANOVA done for Groups 1 and 3 yielded an effect of days ($F_{6/84} = 6.33$, $P < 0.001$) and days with periods interaction ($F_{6/84} = 3.64$, $P < 0.001$). This interaction confirmed that the change from decrease to increase of the rates after CS_{def} termination observed in the course of training is significant. An identical ANOVA for Groups 2 and 4 showed an effect of groups ($F_{1/14} = 21.33$, $P < 0.001$) and periods ($F_{1/14} = 9.35$, $P < 0.01$) indicating significantly lower rates during the C than in A periods.

In subsequent stages of training, when contingencies were changed, differences between rates of responding in A and C periods became unsystematic.

Pattern of responding during CSi presentations

It has been reported previously (25) that during CS_{alim} presentations specific within-trial distribution of responses existed with higher rates of responses in the first than in the second half of the trial. These two 30 s subperiods were labelled B_1 and B_2, summed for each day independently for CS_{alim} and for CS_{def} presentations and compared using the Wilcoxon two-tailed test. These analyses showed that during acquisition the negatively accelerated pattern of within-trial responding was significant in 68% of the comparisons for CS_{alim} and only in 4% of CS_{def} comparisons. During extinction of conditioned enhancement such a pattern of responding was significant in 52% of the comparisons for the previous CS_{alim}, but never for CS_{def} either overtrained or under extinction. The negatively accelerated pattern of responding was maintained in 20% of the comparisons done for CS'_{def} during the reversal learning and was quickly established for CS'_{alim}, being significant in 48% of comparisons.

The negatively accelerated pattern of responding during the CS_{alim} and CS'_{alim} presentations indicate that the first half of the CS_{alim} had

a stronger enhancing effect than the second half. Thus, it may be expected that A-2 × B_1 comparisons will show a greater number of significant enhancements during the CS_{alim} than the A-2 × B_2 comparisons, and these numbers may differ from estimations based on A-B comparisons presented in Figures 1-4. The three kinds of comparisons based on daily A, B, B_1 and B_2 measures for each rat yielded similar results for the acquisition and reversal stages. Only in Group 1 during acquisition did the A-2 × B_1 comparisons show six cases and the A-2 × B_2 comparisons only three cases of significant enhancement of barpressing rate during the CS_{alim} action. On the contrary, clear differences between the three kinds of comparisons were obtained for extinction (Table VI). The A-2 × B_1 comparisons, similar to the A-B comparisons

TABLE VI

Numbers of significant ($P < 0.05$, Wilcoxon test) cases of enhancement of the barpressing rate during the presentations of the previous CS_{alim} in the course of 10 days of extinction estimated by the A−B, A−2×B_1, and A−2×B_2 comparisons based on daily A, B, B_1 and B_2 measures for each rat

Group	CS_{alim} under extinction	Comparisons A−B	A−2×B_1	A−2×B_2
Group 2	Darkness	2	3	0
Group 4	White noise	10	10	5
Group 1	Darkness	3	5	1
Group 3	White noise	10	10	7

presented before, showed the high resistance of the noise CS_{alim} to extinction. The A — 2 × B_2 comparisons revealed that the extinction procedure was successful in weakening the enhancing properties not only of the darkness but also of the noise CS_{alim}.

DISCUSSION

Let us start with the main problem of the present study: stimulus modality effects on conditioned enhancement and conditioned suppression. Although they were observed at all stages of the experiment, clear-cut effects of the stimuli used were observed during the pretest days and during extinction of the conditioned enhancement. The pretest days give information about the unconditioned effects of the to-be conditioned stimuli. The general character of these effects in rats have been reported several times: the first presentations of the acoustic or light stimuli eli-

cited attenuation (8, 13, 27, 28, 30, 31) and during the next presentations as a rule the enhancement of the barpressing responding maintained by food reinforcement was observed (4, 5, 11, 12, 18, 20, 32). Data presented in this paper based on within-subjects comparisons done for each group of rats and testing day independently indicated that barpressing rate was higher during the action of the noise than during the darkness presentations.

On the basis of these inborn predispositions it might be expected that the noise would be more suitable for the CS_{alim} evoking conditioned enhancement, whereas the darkness would be better as the CS_{def} evoking conditioned suppression of barpressing rate. The acquisition stage of the experiment, consisting in differentiation of the two stimuli signalling either food or pain, did not fulfil these expectations. Acquisition of the conditioned enhancement was rapid in any group independent of the stimulus used. Acquisition of the conditioned suppression was retarded only in Group 1 in which the noise was used as the CS_{def}. This finding and significant stimulus effect on conditioned suppression magnitude discovered in the ANOVA are totally dismissed by the fact that Group 2, in which the noise CS_{def} was also used, showed perfect acquisition of the conditioned suppression. It might be concluded that the temporal contiguity between the CS and the event it signals fully determines the behavior evoked by the CS independent of its inborn predisposition.

The stimulus modality effect emerged, however, immediately during the extinction of conditioned enhancement, when the previous contingencies among CS, barpressing and food reinforcement were changed. The noise used before as CS_{alim} elicited significant conditioned enhancement of barpressing during all ten days of extinction, whereas darkness lost such an effect after a few days. It must be stressed that the rats noticed the change in contingencies used, since the barpressing rate decreased the next day after CRF removal. The results suggest that the inborn predispositions of rats to react to the noise with enhancement of the on-going barpressing was responsible for high resistance to extinction of the acquired properties of this stimulus. Darkness was much less effective to evoke such reaction in rats, what was reflected by more rapid weakening of the conditioned enhancement elicited by this CS.

The modality of the stimuli influenced also responding during presentations of the CS_{def} under extinction. In this situation darkness elicited more pronounced suppression than the noise. Any inferences based on this result, however, were weakened by marked differences in the amount of suppression that existed between the groups before extinction. It should be mentioned that not only extinction but also overtraining, although to a lesser extent, weakened the conditioned suppression, and

in both situations the darkness CS_{def} lost its suppressing properties more than the white noise CS_{def}.

The course of reversal learning was strongly influenced by levels of conditioned enhancement and conditioned suppression at the end of the extinction stage of the experiment, which obscured possible stimulus modality effects. In fact, the transformation from conditioned enhancement to conditioned suppression did not show clear dependence on the stimuli used. Nevertheless, it is worthwhile to mention that the training of suppression to the noise CS_{def}, which evoked enhancement to the very end of extinction in Groups 3 and 4, resulted in greater depression of the on-going barpressing than the use of darkness CS'_{def}. This may indicate more difficulty (or perhaps more frustration) involved in the change of the noise from CS_{alim} to CS'_{def} than the similar change in the signalling values of darkness. These differences in the magnitude of the depression of baseline responding resulted in another marked difference between Groups 1 and 2 from one side and Groups 3 and 4 from the other side. Comparisons of the overall $B/(A + B)$ ratios given in Table II and Table IV indicate that the change of the darkness CS_{def} to the CS'_{alim} resulted in greater increase of the ratio values than the similar change of the noise CS.

Summing up, it may be concluded that stimulus modality effects are manifested more distinctly when the signaled meaning of stimuli became ambigous, as during extinction or reversal learning.

There is a question, however, whether the differences between the behavioral effects of the stimuli used presently may be considered as stimulus modality effects or are rather related to specific qualitative aspects of the light offset and the acoustic noise of 70 dB intensity. The between groups comparisons, based on data presented in another study also employing hooded rats, indicate that the light stimulus, an increase in house light intensity, had a stronger unconditioned disruptive effect on on-going barpressing rate maintained by food reinforcement than the acoustic stimulus, 40 Hz click of 70 dB intensity (2). In spite of marked qualitative differences between the stimuli and the level of the on-going barpressing, the unconditioned effects of light and acoustic stimuli were similar in the two studies. Obviously, these similarities in unconditioned effects were related to the modalities of the stimuli and not to the specific characteristics of the stimuli used in the two studies.

It is worthwhile to add that Kamin (14) has also shown that the house light onset has some unconditioned suppressing effect on barpressing behavior of rats and, as a result, conditioned suppression training was somewhat faster to a light CS than to a 80 dB white noise CS. In another study, in which unconditioned effects of the stimuli used were not re-

ported, the magnitude of conditioned suppression acquired during the first four trials with the house light onset as the CS was in between those observed for 60 dB and 80 dB white noise CSi (15).

The other point needing comment is the effectiveness of different methods used for the transformation of associations. The results of the present experiment clearly indicate that extinction procedures, both for conditioned enhancement and conditioned suppression, were less effective than the reversal learning procedure. We have used different methods to weaken conditioned enhancement: series of acute extinction trials (24), chronic extinction (this paper) and reversal learning (25 and this paper). The acute extinction method, introduced by Pavlov, consists in the drastic lengthening of the CS action given without an unconditioned stimulus (reinforcement) and is now termed the flooding method. The chronic extinction method, also introduced by Pavlov, means only one change in the CS presentations namely withdrawal of the unconditioned stimulus (reinforcement). Both of these methods resulted in the weakening of conditioned enhancement, however marked fluctuations in response rates, including statistically significant increases of barpressing after several days of no differences between pre-CS and CS_{alim} rates, were commonly observed. Similar fluctuations occurred during extinction of conditioned suppression. In contrast, during reversal learning, changes in the level of performance were rapid and the magnitudes of daily fluctuations markedly reduced. Generally, it seems that heterogeneous transformations are more effective than homogeneous ones (compare: 22).

The most resistant to extinction are the behavioral effects of CS_{alim} onset. The data obtained during the acute extinction procedure showed that even during the first prolongation of the CS_{alim} this stimulus had lost its enhancing properties. Nevertheless in the following presentations, the onset of the CS_{alim} again evoked significant enhancement of the barpressing rate (24). The results of the present experiment indicate that not only during acquisition but also during extinction was greater enhancement of the barpressing rate observed during the first than during the second half of the CS_{alim}. In experiments with extinction of salivary conditioned responses in dogs a similar difference between the first and the second portions of the CS_{alim} action has been also observed (17, 23). Moreover, the differences in amount of salivation during the two portions of the CS_{alim} were especially pronounced when the CS_{alim} subjected to extinction was presented between other conditioned stimuli reinforced by food ("extinction on the excitatory background" procedure). These differences were smaller when the extinguished CS_{alim} was applied in special sessions during which no other CSi were used ("extinction on the

inhibitory background" procedure). These data, from the series of papers now considered as classical, demonstrated the influence of other conditioned stimuli used in a given experimental situation on the response elicited by a given CS.

In the present study the "excitatory background" for the CS_{alim} was provided by the 2.5 min VI operating all the time during the experimental sessions. This factor may be responsible not only for the very pronounced enhancing effect of the CS_{alim} onset in comparison with the second portion of this stimulus, but also for the low effectiveness of the procedures employed for extinction of conditioned enhancement and rapid transformation of the CS_{def} into CS'_{alim}. The data obtained in experiments employing parallel training of conditioned enhancement and conditioned suppression suggested that the analysis of the interactions between the appetitive and aversive stimuli must also include their effects on the contextual stimuli. The appetitive and aversive stimuli not only elicited certain behaviors, but also determined the general character of the "background", which exerted modifying influences on the behavioral effects of the appetitive and aversive stimuli.

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