EFFECTS OF FOOD DEPRIVATION AND REINFORCEMENT MAGNITUDE ON CONDITIONED SUPPRESSION

JULIAN C. LESLIE¹

NEW UNIVERSITY OF ULSTER

In Experiment I, the responding of rats lever pressing on a variable-interval schedule for sucrose solution was partially suppressed by a variable duration conditioned stimulus followed by shock. When food deprivation was increased, response rates during and before the conditioned stimulus increased monotonically. Varying the concentration of sucrose across blocks of sessions or from session to session in a semi-random sequence had little effect on response rates either before or during the conditioned stimulus. With a fixed sequence of increasing concentrations across a five-session block, increased concentration produced much more rapid increases in response rates before than during the conditioned stimulus. In Experiment II, rats were presented with the same sequence of increasing concentrations across a five-session block. When tested at 80% body weight, response rates increased rapidly as concentration increased, but at 100%, body-weight rates increased only slightly. The effect of a change in body weight in Experiment II thus mimicked the effect of the conditioned stimulus in the latter part of Experiment I. These findings support the view that the effect of a pre-aversive conditioned stimulus is similar to that of a change in food deprivation, but unlike that of a change in reinforcement magnitude.

Key words: conditioned suppression, food deprivation, reinforcement magnitude, lever press, rats

The repeated pairing of a neutral conditioned stimulus (CS) with electric shock results in response suppression during the CS (Estes and Skinner, 1941). Such conditioned suppression has been shown to be a function of CS and shock parameters and the nature of the operant schedule of reinforcement maintaining the response (see reviews by Blackman, 1977; Lyon, 1968). However, its interaction with variables that affect performance on the schedules used to maintain responding has been neglected.

Investigation of such variables is made more relevant by several recent attempts to account for conditioned suppression and other phenomena produced by the interaction of operant and classical conditioning procedures in terms of motivational changes (*e.g.*, Millenson

and de Villiers, 1972a; Rescorla and Solomon, 1967). On such an account, a CS that has been paired with a powerful reinforcer elicits a change in motivation that is reflected in the ongoing operant behaviour. A pre-aversive CS, for example, will reduce the level of appetitive motivation and consequently reduce positively reinforced responding to a rate appropriate to a lower level of motivation. Millenson and de Villiers (1972a) hypothesized that the decrement in motivation produced by a particular CS is constant, *i.e.*, it is independent of the level of motivation preceding its onset. If we wish to test this hypothesis, but avoid the pitfalls inherent in any comparison of rate changes under different conditions and the circularity of inferring the preceding level of motivation from the effect of the CS (Blackman, 1977), we must obtain data on the effects of parametric variation in motivational variables on response rate and the rate change during a pre-aversive CS. The predictions of the motivational interpretation can then be tested against these data. Is the rate change produced by the CS equivalent to a constant decrement in a motivational variable? Are functions relating response rate and the rate during the CS to one variable, *e.g.*, food de-

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privation, the same as for another, *e.g.*, concentration of sucrose reinforcement?

It is usual to distinguish between "motivation" variables, such as food deprivation, and "incentive" variables, such as reinforcement magnitude. Few experiments have systematically investigated the relationship between food deprivation and response rate on the variable-interval (VI) schedules typically used in conditioned suppression studies, although Ferster and Skinner (1957) with pigeons and Clark (1958) with rats showed that rate increased with deprivation over a wide range of values. Parametric data are not available from conditioned suppression studies: Millenson and de Villiers (1972*b*) found that partial satiation resulted in greater relative suppression in rats; Weiskrantz (1953) noted that a large increase in food deprivation reduced the suppression shown by two monkeys.

Reinforcement magnitude is known to affect choice and response rate systematically in concurrent and multiple VI schedules, but few studies systematically varied reinforcement magnitude for a single operant within subjects. However, Schrier (1963) found that in monkeys, response rate increased slightly with sucrose concentration, while Collier and Willis (1961) found that VI rate of rats increased with concentration in a between-groups analysis. Parametric data from conditioned suppression studies are lacking, but Millenson and de Villiers (1972*b*) found that conditioned suppression was greater in sessions where VI reinforcement was an 8% rather than a 32% sucrose solution. However, Hancock and Ayres (1974) failed to replicate this result.

If rewarding brain stimulation is used as the reinforcement for the operant response, then reinforcement magnitude can be varied by altering the intensity of stimulation. This has been done in two studies of conditioned suppression. Both Brady and Conrad (1960) and Russell (1975) found that suppression was attenuated when more-intense brain stimulation was used as reinforcement.

To allow the motivational account to be evaluated, the first experiment in the present study provided data on the effects of parametric variations in level of food deprivation and reinforcement magnitude on VI response rate and conditioned suppression. Partial conditioned suppression that would act as a sensitive baseline was obtained by using a variable

duration CS followed by a moderate-intensity shock. All features of the classical conditioning part of the procedure were held constant throughout the experiment.

EXPERIMENT I

METHOD

Subjects

Eight experimentally naive male hooded rats, obtained from the Oxfordshire Laboratory Animal Colony and 120 days old at the start of the experiment, were housed singly with water always available; they were maintained at the body weight appropriate to the current phase of the experiment by feeding a measured amount of standard diet after each session.

Apparatus

Two standard Campden Instruments CI 140 rat-conditioning chambers mounted in sound-proof housings were used (*cf.* Millenson and Dent, 1971). Only the right levers were operative. Positive reinforcement was 0.1 ml of sucrose solution delivered by a dipper mechanism into a tray behind a clear plastic flap. All sucrose solutions were calculated by weight, the particular concentration used depended on the phase of the experiment. The CS was three 1.2-W lights mounted in a horizontal row above the lever and reinforcement mechanism; these flashed synchronously at 5 Hz. Footshock of 0.3 mA for 0.5 sec was delivered through a grid floor from the scrambled output of two Grason-Stadler E 1064 constant-current shock generators. All phases of the experiment were controlled by an on-line minicomputer, which presented stimuli and recorded data.

Procedure

Phase I. Four subjects (1 to 4) were gradually reduced to 85% and the other four (5 to 8) to 75% of their free-feeding weights. All were then shaped to press the right-hand lever for access to 20% sucrose solution. Over a period of five daily 30-min sessions they were shifted to a schedule on which lever presses were reinforced after a variable interval with a mean of 1 min (VI 1-min). The reinforcer was 3-sec access to 20% sucrose solution, timed from the moment the subject's head pushed open the flap covering the food tray. All sub-

sequent sessions lasted 30 min. Training on this VI 1-min schedule continued for 18 sessions, when all subjects showed a response rate that was stable from day-to-day. The conditions and numbers of sessions experienced by each subject are shown in Table 1.

Phase II. CS presentations were then begun. CS durations of 15, 30, 45, 60, 75, 90, and 105 sec occurred with equal frequency in a random sequence (mean duration = 60 sec). The interval between CSs varied and had a mean of 5 min. After four sessions in which the CS was presented alone (CS habituation), all subsequent presentations of the CS were followed immediately by a US of a 0.3-mA, 0.5-sec shock. This procedure was continued for 20 sessions.

Table 1

Summary of the conditions experienced by each subject in Experiment I.

Phase	Subjects	Sucrose Concentration	Deprivation Level	No. of Sessions
I	1, 2, 3, 4	20%	85%	15
	5, 6, 7, 8	20%	75%	15
II	1, 2, 3, 4	20%	85%	32*
		10%		32*
		5%		32*
	5, 6, 7, 8	20%	75%	32*
		10%		32*
		5%		32*
III	1, 3	10%	100%	10
			95%	10
			75%	15
	5, 6	10%	100%	10
			95%	10
			85%	15
IV	2, 4, 7, 8	16%	85%	6
		8%		6
		4%		6
		2%		6
		0%		6
				6

*Total of both parts of Phase II (see text).

Two methods were then used to manipulate sucrose concentration. First, the concentration was changed to 10% for 20 sessions and then to 5% for a further 20 sessions. Second, sucrose concentration was varied from day to day in a semi-random fashion such that 5%, 10%, and 20% each occurred twice every block of six sessions. This procedure continued for six blocks of six sessions.

Phase III. All subjects were allowed to feed freely for two weeks to redetermine their 100%

body weights. Two subjects from each of the earlier groupings were then arbitrarily selected (1, 3, 5, and 6) and were tested for 10 sessions on the same schedule with 10% sucrose reinforcement. The use of sucrose enabled responding to be maintained without food deprivation. These subjects were then reduced to 95% body weight and tested for a further 10 sessions. Following this, Subjects 1 and 3 were maintained at 75% and Subjects 5 and 6 at 85% body weight while a further 15 sessions were conducted.

Phase IV. The subjects not used in Phase III were reduced to 85% body weight and given 0%, 2%, 4%, 8%, and 16% sucrose solutions as reinforcement on successive sessions of a five-session block. This procedure was continued for six blocks of sessions.

RESULTS

Presentation of the CS alone produced slight suppression, which had habituated almost entirely by the fourth session. Introduction of CS-shock pairings resulted in transient disruption of baseline response rates that disappeared within five sessions. Figure 1 presents suppression ratios, calculated as CS rate/CS rate + Pre-CS rate (Kamin, 1961), for individual subjects in Phase II. The values shown are the means of the last five sessions in each condition when performance was stable. The standard deviations ranged between 5% and 18% of the means. Neither varying sucrose concentration across blocks of sessions (right panel), nor randomly from session-to-session (left panel), systematically affected the suppression ratio. Under the latter conditions, subjects at 75% body weight (dotted lines) generally showed less suppression than those at 85% (solid lines). This was also true at the 20% and 10% concentrations when concentration was varied across blocks of session. The CS and pre-CS response rates also failed to be systematically affected by concentration.

Figure 2 presents the CS and pre-CS response rates of the four subjects (1, 3, 5, and 6) used in Phase III where food deprivation, in terms of percentage body weight, was manipulated. All data are the mean values of the last five sessions in each condition, but well represent performance on individual sessions. The standard deviations ranged between 5% and 15% of the means except for the very low CS rates

Fig. 1. Left panel: suppression ratios of all subjects when sucrose concentration was varied from session to session (Phase II). Right panel: data from Phase II when sucrose concentration was varied across blocks of sessions. Dotted lines indicate subjects at 75% body weight; solid lines indicate subjects at 85%

in the 100% and 95% body-weight conditions. These ranged from 10% to 60% of the means. Both CS rate and pre-CS rate increased with deprivation, but the difference between them does not change systematically. This is shown by Figure 3, which gives the suppression ratios and the absolute rate decreases for all four subjects. On the relative measure of suppression, suppression decreases with decreasing body weight. The ranges of standard deviations for the data of Figure 3 are as follows: suppression ratios greater than 0.2, 5% to 18% of the means; suppression ratios less than 0.2, 15% to 50% of the means; rate decreases, 5% to 22% of the means.

Figures 4 and 5 present comparable data from Phase IV, where sucrose concentration was varied from day to day in a fixed sequence.

In this case, the data are the means of the last two sessions conducted at each concentration and are representative of performance in in-

Fig. 2. Response rates in CS and Pre-CS periods as a function of food deprivation for individual subjects in Phase III.

Fig. 3. Two measures of response suppression as a function of food deprivation for all subjects in Phase III.

dividual sessions. Whereas in Phase II neither method of changing the concentration succeeded in producing consistent changes in pre-CS or CS response rates, this method did succeed in controlling the pre-CS rate. Rate was an increasing function of sucrose concentration (Figure 4), but the rate during CS presentations showed a less-steep increase, and in the case of one subject (4) no increase. Two measures of suppression are presented in Figure 5; suppression ratios were not systematically related to sucrose concentration, but the absolute rate decrease during the CS tended to increase with concentration.

DISCUSSION

The effects on conditioned suppression of changes in food deprivation were different from changes in the sucrose reinforcement for lever pressing. In keeping with earlier findings

Fig. 4. Response rates in CS and pre-CS periods as a function of the sucrose concentration used as reinforcement for individual subjects in Phase IV.

Fig. 5. Two measures of response suppression as a function of sucrose concentration for all subjects in Phase IV.

of Weiskrantz (1953) and Millenson and de Villiers (1972b), relative suppression was less when food deprivation was greater. However, because four values of food deprivation were used in the present study, the relationships between food deprivation and pre-CS rate and CS rate could be examined. Over the range of values studied, pre-CS rate was roughly a linear function of deprivation and rate fell during the CS by about the same amount at each level of deprivation. The effect of the CS can thus be equated with a constant change in deprivation, and this is what would be expected on a motivational interpretation of conditioned suppression.

As in earlier studies, both VI response rate and conditioned suppression were fairly insensitive to changes in sucrose concentration. However, a fixed sequence of increasing concentrations on successive sessions did control pre-CS rate. It was then found that pre-CS rate was an increasing function of sucrose concentration, but CS rate increased only slightly with concentration. This had the result that suppression, as measured by decreased absolute rate, increased with reinforcement magnitude. This is contrary to Millenson and de Villiers' (1972b) earlier findings. Too much importance should not be attached to the shape of the functions relating CS and pre-CS rates to sucrose concentration, because they may simply be a result of the unusual procedure of supplying a greater magnitude of reinforcement on each succeeding session within a block. However, it seems safe to conclude that the effect of the CS is not equivalent to a change in reinforcement magnitude, as measured by sucrose concentration. In various phases of the experiment, CS and pre-CS functions were either both "horizontal" (when concentration affected neither rate) or else diverged (when rate drop during the CS increased with concentration). In neither instance can it be concluded that the effect of the CS is equivalent to a constant change in reinforcement magnitude.

The data suggest that the effect of a pre-aversive CS is equivalent to a change in food deprivation but not a change in sucrose concentration. This argument would be strengthened if it could be shown that the effects of the CS on response rate when sucrose concentration was changed in a fixed sequence (Phase IV), which cannot be explained as equivalent to a change in sucrose concentration, can be

duplicated by a change in deprivation level. If rats are tested with the repeated fixed sequences of increasing concentrations used in Phase IV under two different deprivation conditions, will pairs of diverging functions be produced similar to those in Figure 5? A second experiment tested this possibility.

EXPERIMENT II

METHOD

Subjects

Three experimentally naive male rats of the strain used in Experiment I were used. They were numbered 11, 12, and 13 and kept under the same conditions as the subjects in Experiment I.

Apparatus

This was the same as in Experiment I.

Procedure

Initially, the subjects were shaped to press the right-hand lever for 3-sec access to a 10% sucrose solution. They were then shifted to a VI 1-min schedule over a period of four 30-min sessions. There followed 10 daily sessions on this schedule. Subsequently, the procedure was identical with that in Phase IV of Experiment I, except that there were no CS or US presentations and food deprivation conditions were varied. In each block of five sessions, the reinforcement was successively 0%, 2%, 4%, 8%, and 16% sucrose solution. Four such blocks were conducted while the subjects were on *ad lib* feeding (100% body weight). They were then deprived over a period of three weeks to 80% body weight. Once they had stabilized at 80% body weight, four more five-session blocks were studied.

RESULTS

Figure 7 shows the overall response rates for each subject in each condition. The data presented are the means of the last two sessions conducted in each condition and are representative of performance on individual sessions. As in Experiment I, Phase IV, this procedure again resulted in response rate being an

Fig. 6. Response rates as a function of sucrose concentration at two levels of food deprivation, 100% and 80% body weight, for individual subjects in Experiment II.

increasing function of sucrose concentration when the subjects were at 80% body weight. However, at 100% body weight, the response rates increased much more slowly with concentration. Comparison with Figure 4 shows that the 100% curves in Figure 6 resemble the CS curves in Figure 4. In both Figures, the two curves diverge as sucrose concentration increases.

GENERAL DISCUSSION

The data of these two experiments circumvent some of the problems inherent in a motivational interpretation of conditioned suppression. If we know the shape of the functions relating pre-CS rate and CS rate to a variable that affects the former, then we can see whether the effect of the CS on response rate is the same as that of a constant change in the variable. The question is, can we move the CS curve a certain amount to the left so that it will lie on top of the pre-CS curve?

This can be done with the food-deprivation data (Experiment I, Phase III). The effect of the CS was roughly equivalent to a constant change in deprivation. However, the same cannot be said of the sucrose concentration data. Changes in sucrose in concentration either failed to affect pre-CS rate or CS rate (Experiment I, Phase II) or else only systematically affected pre-CS rate (Experiment I, Phase IV). Experiment II showed that the effect of the CS in the latter case, a reduction in rate that increased with sucrose concentration, was similar to that of a large reduction in food deprivation. To date, motivational interpretations of conditioned suppression have assumed that all parameters that affect the reinforcing value of the operant response will interact with conditioned suppression in the same way. The present experiments show this to be an invalid assumption: the CS produced a rate decrement similar to that produced by a changed food deprivation, but unlike the effect of changing the sucrose concentration.

In those parts of Experiment I where the variable manipulated did affect response rates (Phases III and IV), conditioned suppression was found to be a function of the variable. However, in each case only one of the measures of suppression was related to the variable in an orderly manner. If only Kamin's (1961) relative-ratio measure of suppression had been used, we would have concluded that suppression decreases with increases in deprivation, but is unaffected by sucrose concentration; using only the rate-change measure, our conclusion would have been that suppression increases with concentration and is unaffected by deprivation (see Figures 4 and 6). This emphasizes the danger inherent in the common practice of reporting only relative measures of suppression.

In Experiment I, food deprivation was much the more potent variable and controlled both pre-CS and CS response rates. It is possible that these changes were indirectly produced: food deprivation is closely related to general activity and increases in activity might raise pre-CS and CS response rates. However, procedures that raise pre-CS rates do not generally increase CS rates as much. Brady (1956), using amphetamine treatment, and Blackman (1967), using response pacing procedures, found higher response ratios to be correlated with greater suppression (measured relatively or absolutely). Furthermore, in Experiment II the effect of a reduction in food deprivation could not be interpreted as due to a change in general activity, but was similar to the effect of the CS when the same procedure was used in Experiment I (Phase IV). We may conclude that neither rate dependence nor activity changes can account for the relationship between food deprivation and conditioned suppression found in the present study.

The existence of this relationship is in accord with a motivational interpretation of conditioned suppression, if deprivation level but not reinforcement magnitude is presumed to affect motivation. It is not clear how the present findings can be accounted for by an interfering response account (*e.g.*, Kamin, 1965). On this view, responses elicited by the CS as a result of its pairing with shock interfere or compete with the operant response, thus reducing response rate during the CS. If the competing responses are peripheral respondents, then one would expect the amount of suppression of a given response rate to be independent of the deprivation and reinforcement conditions that generate that response rate. If, on the other hand, the competing responses occur at a central level (*e.g.*, Trapold and Overmier, 1972) it remains to be explained why they interact differently with deprivation and reinforcement magnitude changes.

The techniques of the present study provide a method whereby the relationship of conditioned suppression to other variables presumed to affect response strength could be established. Russell (1975) reported that responding maintained by low-intensity brain stimulation was suppressed more (in terms of relative rate and absolute rate) than responding maintained by high-intensity stimulation given on a fixed ratio 1 schedule. Investigation

of more points on the intensity continuum would be needed before it could be determined whether a pre-aversive CS has an effect similar to that of reduction in brain-stimulation intensity.

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