CONDITIONED SUPPRESSION OF COUNTING BEHAVIOR IN RATS¹

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Three rats were trained on a schedule in which a response on lever B was reinforced only if it was preceded by a minimum number of consecutive responses on lever A. The minimum requirement was 27 A responses for Rat 1, and 20 A responses for Rats 2 and 3. The schedule maintained high rates of responding on lever A, and a slow, spaced pattern of responding on lever B. The mean number of consecutive responses on lever A was slightly greater than the minimum required. The effect of superimposing on this behavior a stimulus that ended with an unavoidable shock was the suppression of responding on both levers during the pre-shock stimulus. Responses on lever A were more suppressed, and the proportion of relatively short response runs on lever A during the pre-shock stimulus increased. With all three rats, the mean number of consecutive responses on lever A during the pre-shock stimulus decreased to a value below the minimum requirement for reinforcement of the subsequent B response.

The effects on operant behavior of a stimulus that precedes an unavoidable shock were first studied by Estes and Skinner (1941). They found that responding maintained by a schedule of food reinforcement decreased in the presence of the pre-shock stimulus. This suppressive effect has been demonstrated with many schedules of food and water reinforcement, and the behavioral phenomenon has come to be known as conditioned suppression (Lyon, 1968). However, when the Estes-Skinner procedure is superimposed on the behavior maintained by schedules that differentially reinforce low rates of responding (DRL), the results have been equivocal. Leaf and Muller (1964) found that DRL responding was suppressed during a pre-shock stimulus, but Finocchio (1963) and Blackman (1968a) reported an acceleration of DRL responding in certain conditions. The shock intensity used by Blackman in demonstrating this effect was relatively low, but was nevertheless sufficient to produce reliable suppression of behavior maintained by other schedules of reinforcement. Many experimenters have observed that

repetitive sequences of collateral behavior, *i.e.*, behavior not specified by the reinforcement schedule, sometimes accompany DRL responding, and that when such behaviors occur they appear to mediate the recorded DRL responses (*e.g.*, Hodos, Ross, and Brady, 1962; Laties, Weiss, Clark, and Reynolds, 1965). Collateral behaviors that may mediate DRL responding have not been formally measured in conditioned suppression studies, although incidental observation (Blackman, 1968a) suggests that such behaviors may be disrupted by a pre-shock stimulus.

One way of illuminating the effects of the Estes-Skinner procedure on DRL responding and its collateral behavior is to superimpose it on behavior maintained by a schedule of reinforcement that simulates both DRL responding and collateral behavior. Millenson (1966), using pigeons, simulated variable-interval behavior by using a two-key situation in which responses on one key (B) were reinforced only if preceded by a variable number of responses on another key (A). This procedure resulted in a pattern of responding on key B that closely resembled that generated by a variable-interval schedule. The present experiment attempted to simulate DRL behavior in a similar way using a schedule employed by Millenson as a training procedure. This required that a minimum number of consecutive responses on one lever (A) precede a response

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on another lever (B) for a reinforcer to be delivered (such a schedule has been termed a "counting" schedule, Mechner and Guevrekian, 1962). It was anticipated that this schedule would generate a behavioral baseline against which the effects of the Estes-Skinner procedure might be assessed not only on "DRL-like" responding (lever B) but also on collateral behavior (lever A).

METHOD

Subjects

Three experimentally naive female rats of the Wistar strain were housed individually with water freely available in their living cages but not in the test chamber. Each rat was approximately 200 days old at the beginning of the experiment and was maintained at 80% of its free-feeding weight. The rats were approximately 22 hr food-deprived at the start of each experimental session, except when there were two sessions per day.

Apparatus

The test chamber was a standard Grason-Stadler two-lever rat station (model E3125B) mounted in a sound attenuating chest. A 10-W houselight illuminated the chamber throughout each experimental session. White noise (the pre-shock stimulus) was delivered from a Grason-Stadler E901B generator through a small speaker located beneath the lever to the left of the food hopper. Standard rat food in the form of 45-mg pellets (P. J. Noyes Co.) was the reinforcer. Shock was delivered through the grid floor from a Grason-Stadler (E1064) shock generator and associated scrambler. The experiment was arranged by means of conventional electro-mechanical relays and timers; responses and reinforcements were recorded on digital counters and digital printers. Two cumulative recorders provided continuous displays of the rats' bar-pressing behavior.

Procedure

In the preliminary training phase, there were two sessions daily; each session terminated when 120 reinforcers had been delivered. The rats were magazine-trained, then presses on the lever to the left of the food hopper (lever B) were conditioned by delivering a pellet of food after each response on lever B. Next, reinforcement was made dependent on a re-

sponse on lever B (B response) that followed at least one response on lever A (A response). The A response requirement was gradually increased until a minimum of 20 was required before a B response was followed by reinforcement. Each B response reset the A response requirement to its maximum value so that a B response that followed fewer than 20 consecutive A responses was never reinforced.

The session length was then changed to 60 min, and the number of sessions per day was reduced to one. It soon became clear that responding could not be maintained for 60 min with two of the rats. Rat 1 responded at such a high rate, and so effectively, that it became satiated and ceased responding before the end of the session. To circumvent this, the A response requirement was gradually increased for Rat 1 until responding was maintained throughout each session; this resulted in a final A response requirement of 27. Rat 2, on the other hand, ceased responding on both levers approximately 15 min before the end of several consecutive 60-min sessions. However, there was no evidence for the gradual behavioral changes normally associated with either satiation or extinction. Therefore, the A response requirement of 20 was not altered for Rat 2, but the session length was changed to 40 min for this animal only and remained so for the rest of the experiment.

When all rats had been exposed to these final experimental arrangements for at least 45 daily sessions, white noise was introduced for 2-min periods regularly once every 10 min. The first noise period started 4 min after the beginning of each session; there were six noise periods each session for Rats 1 and 3, but only four per session for Rat 2.

After 20 sessions during which the periods of noise were presented as above, each period was terminated with an unavoidable electric shock (0.3 mA, 0.2 sec nominal values). The rats were exposed to these conditions for the remaining 20 sessions of the experiment.

RESULTS

The term "run length" is used to describe the number of A responses intervening between successive B responses; for example, with Rat 1 only a run length of 27 or more A responses arranged for a subsequent B response to be reinforced.

The schedule used typically produced high overall rates of responding on lever A and slower, spaced responding on lever B. Figure 1 presents typical cumulative response records to illustrate these patterns of operant behavior for Rat 2. The record shown for lever B is arranged in the conventional way, with oblique marks to denote reinforcement. The segment shown for lever A was produced at the same time and corresponds with that shown for lever B. The oblique marks on the A record denote the emission of B responses and the event record between the two cumulative response records shows when B responses were followed by reinforcement.

The upper part of Table 1 summarizes the data obtained from the last five sessions during which periods of noise were presented without shock. Mean A and B response rates and mean run lengths summarize the behavior emitted in the absence of the noise (control) and in its presence (noise). A comparison of responding during the noise and in its absence is provided

Fig. 1. Cumulative response records illustrating the lever-pressing behavior maintained by the schedule of reinforcement for Rat 2. After at least 20 consecutive responses on lever A, a response on lever B produced reinforcement. Oblique marks on the lever A record indicate responses on lever B. Reinforcements are indicated on the event record below the lever A record, and by oblique marks on the lever B record.

by the inflection ratio. This was calculated for the behavior on each lever by dividing the mean response rate during the noise by the mean control rate for each whole session. Thus, acceleration of responding during the noise would be represented by a ratio greater than 1.00 and conditioned suppression by a ratio smaller than 1.00. Table 1 shows that the control mean run lengths were in all cases slightly greater than the minimum requirement for reinforcement. This table also reveals that the periods of noise alone had an effect on the two patterns of lever-pressing behavior; for each rat, and particularly for Rat 3, response rates on both levers were higher during noise periods. These behavioral changes took the form of a general increase in response output, with approximately proportional rises in both response rates. The run length data show that the relationship between A and B responses did not change markedly during the noise.

The lower part of Table 1 shows the data obtained from the last five sessions of the experiment when each period of noise ended with an unavoidable shock. Again, the control data summarize performance in the absence of the noise. With Rat 1, these control data are similar to those displayed in the upper part of Table 1. However, the control rates of responding of Rat 2 on both levers are somewhat lower than the corresponding data in the upper part of Table 1, and, finally, for Rat 3 the control rates of responding are appreciably higher in these final sessions of the experiment. Despite these differences, the mean run length data for control conditions reveal that the behavior of each rat maintained its overall organization in terms of the relationship between A and B responses, with mean run lengths greater than the minimum requirements for reinforcement.

Greater changes in behavior occurred during the pre-shock stimulus, for the behavior of each rat on both levers was suppressed during noise periods. This is shown by the mean response rate data for the noise condition and is also expressed in the lower part of Table 1 in the form of inflection ratios. These ratios show that not only was responding on both levers suppressed during the pre-shock stimulus but that, with all three rats, responding on lever A was more suppressed during the noise than was responding on lever B. The

Table 1

The upper frame shows mean A and B response rates and mean run lengths obtained from the last five sessions during which each noise period ended without shock. Inflection ratios for responding on each lever are also shown. The lower frame shows the corresponding data for the last five sessions during which each noise period ended with an unavoidable shock.

Rat	A:B Response Requirement	Mean A Rate (responses per min)		Mean B Rate (responses per min)		Mean Run Length		Mean Inflection Ratios	
		Control	Noise	Control	Noise	Control	Noise	A	B
No shock									
1	27:1	130.4	156.2	4.6	5.0	28.3	31.2	1.20	1.09
2	20:1	121.4	137.7	5.7	5.8	21.3	23.7	1.13	1.02
3	20:1	57.3	87.6	2.4	4.0	23.9	21.9	1.53	1.67
Shock									
1	27:1	128.3	72.3	4.7	3.5	27.3	20.7	0.56	0.74
2	20:1	102.8	45.8	4.0	3.2	25.7	14.3	0.45	0.80
3	20:1	83.4	43.6	3.6	2.3	23.2	19.0	0.52	0.64

differential suppression of the two patterns of behavior was correlated with a decrease in the mean run length during the noise stimulus; indeed, with all three rats, the mean run length decreased to a value less than the minimum requirement for reinforcement.

This latter finding is elaborated in Figure 2, which shows the relative frequencies of run lengths in the presence and the absence of the pre-shock stimulus. It should also be noted that run lengths recorded in the first category were in fact almost always 0, representing two or more B responses emitted with no intervening A responses. In general, there was more variability in run lengths during the pre-shock stimulus as shown by flatter distributions. With each rat there was a slight increase in the relative frequency of exceptionally long runs. It is possible that this may have resulted from two or more trains of A responses separated by a pause but with no intervening B response. The main effects of the pre-shock stimulus on the distribution of run lengths are clear, however: the modal run lengths shifted from values equal to or greater than the minimum requirement to values less than that requirement, and there was an increase in the relative frequency of run lengths shorter than the modal values.

Finally, Figure 3 shows typical cumulative response records to illustrate the effects of the pre-shock stimulus on the counting behavior maintained in this experiment. These records were obtained in the same way as those shown in Figure 1; however, the response pens were

offset during the periods of noise, and the oblique marks are reversed in direction during that time. The main effects reported above can be seen in these records: conditioned suppression of both A and B responses with comparatively less suppression of B responding and a decrease in run length during the pre-shock stimulus (as revealed by the shorter vertical distances between the oblique marks on the A response record).

DISCUSSION

The schedule associated with lever A was essentially a fixed-ratio schedule. It produced sustained rates of responding on that lever, except for brief pauses that were observed after a B response, whether a reinforcer was delivered or not. The records of A responding shown in Figures 1 and 3 therefore resemble those reported for other fixed-ratio schedules (*e.g.*, Ferster and Skinner, 1957). The cumulative records of B responses shown in Figures 1 and 3, on the other hand, display a spaced pattern of responding that closely resembles that produced by a schedule that differentially reinforces low rates of responding (*cf.*, the DRL records shown by Laties *et al.*, 1965).

It is not clear why periods of noise alone exerted such effects; nor is it clear why the control response rates of Rat 3 should have increased between that phase of the experiment and the final phase when each noise period ended with an unavoidable shock. However, these occurrences do not affect the

Fig. 2. Relative frequencies of specified run lengths in the absence (filled circles) and presence (open circles) of the pre-shock stimulus. The vertical lines denote the minimum run length requirement for each rat. These data were obtained from the last five sessions of the experiment.

within-session method of assessing the effects of the pre-shock stimulus as used here. It is clear that in the final phase of the experiment, responding on both levers was suppressed during the pre-shock noise stimulus in comparison with the rest of each session. It is also clear from the suppression ratios shown in the lower part of Table 1 that with all three animals, B responding was less severely suppressed during the pre-shock stimulus than A responding.

There may be a number of reasons why A responding was more suppressed during the pre-shock stimulus. DeCosta and Ayres (1971) reported that responses in close temporal prox-

Fig. 3. Cumulative response records illustrating the effects of the pre-shock stimulus on responding on both levers (Rat 2). The response pens were offset during the pre-shock stimulus. Oblique marks on the lever A record indicate responses on lever B. Reinforcements are indicated on the event record below the lever A record, and by oblique marks on the lever B record. (N.B. The direction of the oblique marks on both response records is reversed during a period of pre-shock stimulus.)

imity to reinforcement were less susceptible to disruption by a pre-shock stimulus. In the present study, only B responses were followed by immediate reinforcement, and they were therefore in closer proximity to reinforcement than were A responses. Also, A response rates in the present experiment were much higher than B response rates; Blackman (1968b) reported that high response rates were generally more suppressed during a pre-shock stimulus than lower rates of responding. However, in Blackman's experiment the different response rates were generated by schedules in which reinforcement frequency remained constant; in the present experiment, A responses were never directly reinforced. Finally, it may be noted that since A responding accounted for a relatively large proportion of the time spent

in the experimental situation, there was a greater probability that the delivery of shock might coincide with the emission of an A response; such adventitious punishment might contribute to the greater suppression of A responding.

The behavior generated on lever A has been likened to fixed-ratio behavior. Lyon (1964) studied pigeons in such a situation in which every one hundred-fiftieth response was reinforced, and found that the continued emission of operant behavior during a pre-shock stimulus depended on the proportion of the fixed-ratio completed when the stimulus was presented. If only a small proportion of the response requirement had been emitted, complete conditioned suppression resulted; if a large proportion had been emitted, responding continued during the pre-shock stimulus, but only until the delivery of the next reinforcer. In the present experiment, some analogous effects were observed. For example, the A response record of Figure 3 shows a pattern of behavior during the second pre-shock stimulus reminiscent in some respects of Lyon's finding. When the noise period began, the rat completed the run of A responses in which it was then engaged and then stopped responding. However, the pause in this case followed an unreinforced B response, and responding began again, continuing through the remainder of the noise-period, despite the delivery of a reinforcer.

The schedule reported here specified a relationship between A and B responses, and it is clear from the run-length distributions during the control periods that the rats' behavior was adapted to this relationship. It may therefore be inappropriate to consider the response rates independently, and may be more useful to compare the present findings with other conditioned suppression studies in which relationships between two operant responses are specified. Blackman (1970a) studied the effects of a pre-shock stimulus on behavior maintained by a two-lever DRL schedule. A response on one lever (B) was reinforced only if a minimum specified time had elapsed since a response on another lever (A). Distributions of the A-to-B elapsed times resulting from this schedule resembled the control run-length distributions obtained in the present experiment. There are further similarities between the two experiments when the effects of the condi-

tioned suppression procedures are compared. In both cases, A responding was more suppressed than B responding during the pre-shock stimulus. Furthermore, the shift reported above in modal run lengths during a pre-shock stimulus is analogous to the changes in the A-to-B elapsed-time distributions reported in the earlier study, with both distributions shifting towards smaller values. One important feature of Blackman's (1970a) study was a large increase in the relative frequency of inappropriate B responses (B responses preceded by no intervening A responses) during the pre-shock stimulus. In the present experiment, only one subject (Rat 2) showed a similar effect; the increase in the relative frequency of run lengths in the 0 to 3 category during the noise stimulus with this rat (see Figure 2) in fact largely reflects an increased proportion of B responses made with no intervening A response, for there were few recorded run lengths of 1, 2, or 3 responses. However, it is difficult to compare this finding with one animal and Blackman's previous report of substantial increases in inappropriate B responses, for the previous study incorporated stimuli that signalled which of the two responses was appropriate at any given moment, which was not the case in the present experiment.

As noted earlier, the temporal patterning of B responses was reminiscent of DRL behavior, though mediated by "counting" behavior on Lever A. Hodos *et al.*, (1962) and Laties *et al.*, (1965) reported that DRL behavior may be accompanied by patterns of collateral behavior that are not specified by the schedule, but that appear to mediate the DRL responding. These investigators also reported that interference with these patterns of collateral behavior impaired the efficiency with which DRL responses were spaced. When investigating the effects of the Estes-Skinner procedure on single-lever DRL behavior, Blackman (1968a) observed that collateral behaviors disappeared during periods of a pre-shock stimulus, and suggested that this might be related to the disruptions of operant lever pressing that occurred at the same time. In the present experiment, the mediating responding on lever A did not disappear during the pre-shock stimulus, but mean run length decreased and A responding was more severely suppressed than B responding. The increase in the proportion of unreinforced B responses during the pre-

shock stimulus may be analogous to the increased proportion of reinforced single-lever DRL responses reported by Blackman (1968a) and to the increased proportion of unreinforced B responses in the two-lever DRL situation (Blackman, 1970a). It is possible that the effects of a pre-shock stimulus on DRL behavior may depend in part on the effects of that stimulus on patterns of mediating behavior, whether or not such behavior is specified by the schedule of reinforcement.

Stein, Hoffman, and Stitt (1971) used observational techniques to study patterns of collateral behavior that regularly accompanied variable-interval responding in the pigeon, although the collateral behavior was not specified by the schedule of reinforcement. It was reported that these collateral behaviors generally decreased in frequency during a pre-shock stimulus, and it was suggested that the Estes-Skinner procedure caused the birds to "freeze" during this stimulus, which was therefore described as producing a "general inhibitory effect on ongoing overt activity, including key-pecking". Such an account may not seem entirely appropriate to the present results, however, for the major finding was not simply suppression of lever-pressing behaviors during the pre-shock stimulus, but disruption of the relationships between responding on lever A and lever B.

Blackman (1970b, 1972) has attempted to relate the effects of a pre-shock stimulus on operant behavior to the concept of stimulus control. For example, the increase in the proportion of inappropriate B responses in the two-lever DRL situation (Blackman, 1970a) occurred although exteroceptive stimuli signalled which of the two responses was appropriate; to this extent, established relationships between environmental stimuli and operant behavior were impaired. In the present experiment, one could argue that runs of A responses set the occasion for a B response, and that the impairment in the established relationships between the two behaviors was similar in some respects to a deterioration in stimulus control. The changes in A-to-B delays in the two-lever DRL situations might perhaps be attributed to a similar process. In short, it may be that a pre-shock stimulus may serve to impair schedule control by disrupting the established relationships between a given pattern of behavior and other events that set the occasion for or con-

trol the emission of that behavior. The discrepancies in the results of previous experiments concerning the effects of conditioned suppression procedures on DRL behavior may be due, in part, to a failure to establish the degree to which collateral behaviors are related to the responses specified by the schedule.

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