**THE EFFECTS OF *d*-AMPHETAMINE ON THE
TEMPORAL CONTROL OF OPERANT RESPONDING
IN RATS DURING A PRESOCK STIMULUS**

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The operant behavior of six rats was maintained by a random-interval schedule of reinforcement. Three-minute periods of noise were superimposed on this behavior, each period ending with the delivery of an unavoidable shock. Overall rates of responding were generally lower during the periods of noise than in its absence (conditioned suppression). These suppressed response rates also exhibited temporal patterning, with responding becoming less frequent as each noise period progressed. The effects of *d*-amphetamine on this behavioral baseline were then assessed. In four animals the relative response rates during the noise and in its absence suggested that the drug produced a dose-related decrease in the amount of conditioned suppression. However, this effect was often due to a decrease in the rates of responding in the absence of the presock stimulus, rather than to an increase in response rates during the stimulus. Temporal patterning in response rates during the presock stimulus was abolished, an effect that was interpreted in terms of rate-dependent effects of *d*-amphetamine. This study thus extends rate-dependent analyses of the effects of amphetamines to the patterns of operant behavior that occur during a presock stimulus, and which have been discussed in terms of the disrupting effects of anxiety on operant behavior.

Key words: conditioned suppression, temporal control, *d*-amphetamine, lever press, rats

Operant behavior maintained by a schedule of intermittent food or water reinforcement often decreases in frequency during a stimulus that precedes an unavoidable shock, a finding first reported by Estes and Skinner (1941). This behavioral phenomenon has been termed conditioned suppression (see review by Lyon, 1968), and has sometimes been attributed to disrupting effects of anxiety (*e.g.*, Estes and Skinner, 1941) or of a conditioned emotional response (*e.g.*, Kamin, 1965). Experimental investigations of conditioned suppression have identified many of the controlling variables that determine the amount of behavior during a presock stimulus (Blackman, 1972; Davis, 1968; Lyon, 1968).

The effects of drugs on conditioned suppression have been frequently investigated, especially in the context of identifying the effects of drugs thought to affect anxiety (see reviews by Kelleher and Morse, 1968 and Millenson and Leslie, 1974). One possible problem in assessing such effects was identified by Millenson

and Hendry (1967), who showed that when a 2-min presock stimulus was superimposed on a variable-interval schedule of food reinforcement, the operant behavior exhibited by the rats during the stimulus showed a marked temporal patterning: response rates became progressively more suppressed throughout the presock stimulus. Millenson and Leslie (1974) pointed out that this temporal organization of behavior during a presock stimulus may make it difficult to interpret the effects of a drug on conditioned suppression. Thus, a drug may reduce overall suppression during a presock stimulus largely by affecting the temporal control of behavior. Furthermore, since it has been established (Kelleher and Morse, 1968; Sanger and Blackman, 1976) that the effects of some drugs are dependent to a large extent on the rate of operant responding in control conditions, any temporal patterning of responding during a presock stimulus adds to the complexity of interpreting drug effects on conditioned suppression.

The present study investigated the effects of *d*-amphetamine on the temporal control of operant behavior during a presock stimulus. Among investigations of the effects of the amphetamines on conditioned suppression,

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markedly divergent results have been reported (Brady, 1956; Cappell, Ginsberg, and Webster, 1972; Lauener, 1963; Miczek, 1973). It is known, however, that the amphetamines consistently produce marked changes in the temporal patterning of operant behavior maintained by schedules of reinforcement such as fixed-interval (Branch and Gollub, 1974; Kelleher and Morse, 1968; McMillan, 1968, 1969; Smith, 1964) and differential reinforcement of low rates of responding (Kelleher, Fry, Deegan, and Cook, 1961; Sanger, Key, and Blackman, 1974; Schuster and Zimmerman, 1961; Segal, 1962; Sidman, 1955). Moreover, the effects of these drugs on such behavioral baselines have been interpreted as being dependent on the rates of responding characteristic of saline conditions (Kelleher and Morse, 1968; Sanger and Blackman, 1976).

METHOD

Subjects

Six male, hooded rats were used. Each was individually housed with free access to water and was maintained at approximately 85% of its pre-experimental body weight, which was within the range of 300 to 380 g. Three animals (R1, R2, and R3) had served in a previous experiment concerned with the effects of drugs, including *d*-amphetamine, on behavior maintained by modified variable-interval schedules. However, they had received no drug injections for over 50 days before drug administration was initiated in the present experiment. The three other rats had not served in previous experiments.

Apparatus

Three standard Lehigh Valley Electronics operant test chambers were used. Each was housed in a sound- and light-proof cubicle and was fitted with two levers and a dispenser for delivery of 45-mg food pellets (Campden Instruments Limited) to the rats. Only presses on the left-hand lever had scheduled consequences in the present experiment. The experiment was controlled on line by a PDP-9 computer (Digital Equipment Corporation) programmed in a version of ACT, a language designed for use in experimental psychology (Millenson, 1971). Recording of responses was also achieved by the computer and cumulative re-

corders were used to provide a continuous record of ongoing behavior.

Procedure

The experimentally naive rats were trained to take food pellets from the food tray and were then exposed to a schedule on which each depression of the lever was followed by delivery of a pellet. After three sessions on this schedule, a random-interval 32-sec (RI 32-sec) schedule was introduced (Millenson, 1963). This schedule was generated by the computer so that the minimum interval between reinforced lever presses was 4 sec and the maximum 64 sec. The rats were exposed to approximately 30 sessions of the random-interval schedule; sessions were given at the same time daily and were 60 min in duration. The three rats with experimental histories were exposed to the random-interval schedule for approximately 20 sessions.

Following this initial exposure to the random-interval schedule, experimental sessions continued as before, but several presentations of white noise were given to each rat during each session. These stimulus presentations lasted for 3 min and were scheduled to occur at irregular intervals during each session, with the minimum time between termination of one presentation and initiation of the next being 4-min. Five, six, or seven presentations of the noise stimulus occurred during each session. The noise was presented alone for one session to ensure that it had no disruptive effect on ongoing responding. In subsequent sessions, each period of the noise terminated with the presentation of a brief, unavoidable electric footshock. The shock intensity was 0.25 mA of 0.5 sec duration. After 15 sessions, during which it was found that this shock produced a small and variable amount of response suppression during the stimulus, the shock intensity was increased to 0.5 mA and maintained there throughout the rest of the experiment. After 20 to 25 sessions of this final procedure, drug administration was begun.

d-Amphetamine sulfate was administered in doses of 0.25, 0.5, 1.0, and 2.0 mg/kg. The drug was dissolved in physiological saline and injected intraperitoneally in a volume of 2 ml/kg approximately 5 min before the start of a session. Doses were given in an irregular order and each animal received each dose on two or

three occasions. At least three nondrug sessions intervened between successive drug sessions and saline injections were given before most nondrug sessions. Control data were obtained from the sessions that immediately preceded drug sessions and the effects of the preshock stimulus were assessed by comparing behavior during the stimulus presentations with behavior during the 3-min periods immediately preceding each presentation.

RESULTS

The random-interval schedule maintained steady rates of responding throughout each session typical of behavior maintained by these and variable-interval schedules (Ferster and Skinner, 1957; Millenson, 1963). When the 3-min periods of white noise ended with 0.25-mA footshock, the behavior during the noise was variable and inconsistent, as noted above. However, when 0.5-mA footshock was presented, marked suppression of responding during the white noise occurred with five of the six rats. With the sixth animal (R 4), response rates during the preshock stimulus were suppressed only slightly. Figure 1 shows typical cumulative records for one complete session for each of the six animals. The 3-min preshock periods are shown by deflections of the pen. It is clear from these records not only that there were overall reductions in response rates during the stimulus presentations but that the responding that did occur during these periods showed a temporal patterning. During the early part of each 3-min stimulus there was little evidence for any reduction in response rate, but towards the end of each stimulus responding decreased.

The effects of *d*-amphetamine were first assessed in terms of a suppression ratio, a relative measure that has been widely used to quantify the disrupting effects on behavior of a preshock stimulus (Stein, Sidman, and Brady, 1958). This ratio was calculated by dividing the response rate during the stimulus presentations by the rate taken from the 3-min periods immediately preceding each presentation. Thus, a ratio of 1.00 indicated no suppression, while ratios below 1.00 indicated conditioned suppression during the stimulus presentations. Figure 2 shows the effect of *d*-amphetamine on suppression ratios. In four animals (R1, R2, R3, and R6) the drug produced clear, dose-related reductions in response suppression.

With R4 there appeared to be increased suppression, particularly with the lower doses (0.25, 0.5 mg/kg) of the drug. The various doses of *d*-amphetamine had no consistent effect on suppression ratios obtained from R5.

The effects of the drug were next assessed in terms of changes in absolute response rates during the preshock stimulus and during the prestimulus control periods. It can be seen from Figure 3 that the drug affected response rates both during the preshock stimulus and during the control periods. Random-interval response rates during the control periods showed a dose-related decrease with five of the six subjects, but the drug had variable effects on response rates during the stimulus. With some animals, suppressed rates were increased (R1, R2) and in others rates were decreased (R3, R4).

To quantify the temporal patterning of responding that occurred during the preshock stimulus, each 3-min stimulus was divided into six 30-sec segments. A Mathematical Index of Curvature (Fry, Kelleher, and Cook, 1960) was then calculated from the response rates in these segments for each rat in each session. An index of 0 indicated a constant response rate throughout the 3-min stimulus periods, while indices with negative values (to a maximum of -0.83) indicated negatively accelerated responding during the stimulus, and positive indices (to a maximum of 0.83) indicated positively accelerated responding. Figure 4 shows the effect of *d*-amphetamine on this index. The drug consistently changed the value of the index, showing that the temporal organization of responding during the stimulus was altered. In every animal, at least one dose of *d*-amphetamine changed the index from a negative to a positive value, showing that on these occasions, responding during the stimulus was no longer negatively accelerated as in control conditions but was, in fact, positively accelerated. Figure 5 shows cumulative records to illustrate the effect of the drug at a dose of 1.0 mg/kg, except in the case of R6. For this rat, the record shows behavior after a dose of 0.5 mg/kg, since 1.0 mg/kg greatly reduced responding at all times during the session (see Figure 3). Comparison of the records presented in Figure 5 with those in Figure 1 shows that the drug markedly altered the patterning of responding seen during the preshock stimulus.

Fig. 1. Sample cumulative records showing one complete session of the random-interval schedule with superimposed stimulus shock pairings for each of the six rats under control conditions. The 3-min preshock stimulus periods are indicated by deflections of the pen. Presentations of reinforcers are not shown.

To investigate the possibility that the actions of *d*-amphetamine on responding during the preshock stimulus were dependent on the

control response rates during the segments of the stimulus, the response rates during these segments after administration of the 1 mg/kg

Fig. 2. Dose-response curves showing the effects of *d*-amphetamine on suppression ratios in individual rats. The ratios were calculated by dividing the response rates during the prestimulus periods by the rates during the preshock stimulus periods. Thus, a ratio of 1.00 indicated that the stimulus had no effect on response rate; a ratio of 0 indicated complete suppression during the stimulus. The points and vertical lines show the means and ranges of two or three determinations, except for the points and vertical lines at C, which show the mean and range of all control values.

dose were converted to percentages of the corresponding control rates taken from the preceding session. The log of each of these values was then plotted against the log of the corresponding control rate. This procedure has been used on a number of occasions for investigating rate-dependent drug effects on behavior maintained by fixed-interval schedules (*e.g.*, Kelleher and Morse, 1968). Figure 6 shows these graphs for each of the six animals. The points fit relatively closely to straight lines that were fitted by the method of least squares. This linear relationship indicated that the effects of this dose of *d*-amphetamine were directly related to control response rates. In general, high response rates that occurred early in the periods of preshock stimulus were decreased, while the lower rates from later segments of the stimulus were increased.

Fig. 3. Effects of *d*-amphetamine on response rates during the prestimulus periods (—●—) and during the preshock stimulus presentations (—○—). The points and vertical lines show the means and ranges of two or three determinations, except for the points and vertical lines at C, which show the mean and range of all control values.

DISCUSSION

The effects of *d*-amphetamine on conditioned suppression were analyzed in several ways in this study. When the transformed data of suppression ratios were considered, the drug appeared to produce a dose-related decrease in conditioned suppression (Figure 2). However, the untransformed data of response rates in the presence and absence of the preshock stimulus indicated (Figure 3) that the drug produced a dose-related decrease in the rates of responding of the rats in the absence of the preshock stimulus. This finding is consistent with the results of several published reports using variable- or random-interval schedules of reinforcement (*e.g.*, Dews, 1958; Hearst, 1961; Sanger and Blackman, 1975) and points to the dangers of interpreting the effects of drugs on conditioned suppression merely in terms of suppression ratios (Blackman, *in press*).

More detailed analyses of rates of responding during the preshock stimulus in the

Fig. 4. Effects of *d*-amphetamine on the Index of Curvature calculated from response rates during the preshock stimulus periods. The Index can take values from +0.83 (positive acceleration) through 0 (constant response rate throughout the stimulus periods) to -0.83 (negative acceleration). The points and vertical lines show the means and ranges of two or three determinations, except for the points and vertical lines at C, which show the mean and range of all control values.

present experiment showed a consistent temporal patterning such that response rates were relatively high early in the stimulus and decreased to very low rates by the end of the stimulus, when the shock was presented (Figures 1 and 4). These results are consistent with those obtained by Millenson and Hendry (1967), who studied response rates during 15-sec segments of a 2-min preshock stimulus. The effects of the various doses of *d*-amphetamine on this patterning of responding in the present experiment were measured in terms of the Index of Curvature (Figure 4), which showed that the drug reduced the negative acceleration of response rates and at some doses even changed this negative acceleration to a small positive acceleration. In general, the changes in the Index of Curvature were similar to those obtained in experiments that studied the effects of amphetamines on the temporal control of behavior in fixed-interval schedules of reinforcement (*e.g.*, Branch and

Gollub, 1974) except that in such cases, of course, the drug reduced positive acceleration in the pattern of responding.

The rate-dependent analysis presented in Figure 6 provided a more thorough description of the effects of one dose of *d*-amphetamine on response patterning during the preshock stimulus. Dews (1958) first hypothesized that one of the important variables determining the behavioral actions of amphetamine is the rate at which the behavior under investigation is emitted in control conditions, low response rates being increased and high rates decreased. There is now considerable evidence to support this general hypothesis (see reviews by Kelleher and Morse, 1968; Sanger and Blackman, 1976). Much of this evidence has been obtained from studies in which the actions of amphetamines have been studied on temporal patterning of responding maintained by fixed-interval schedules (Barrett, 1974; Branch and Gollub, 1974; Kelleher and Morse, 1968; Leander and McMillan, 1974; McMillan, 1968, 1969; Smith, 1964). In these studies, the drug's effects have typically been studied by segmenting the fixed intervals and comparing response rates during these segments after drug administration with the corresponding rates under control conditions. Such analyses generally produce straight-line functions relating the log of the control response rate with either the log of this rate after drug administration or the log of this rate converted to a percentage of the control rate. In the present experiment, a similar method of analysis using response rates during the 30-sec segments of the preshock stimulus also showed a direct relationship between the effects of one dose of *d*-amphetamine and control response rates. These results are thus consistent with those obtained in previous studies, although a different procedure was used to obtain the range of response rates.

It is of interest to compare the present results with those of studies that have investigated the actions of amphetamines on operant responding maintained at low rates by punishment procedures. Such studies have found that amphetamines further reduce low rate of punished responding (Cook and Davidson, 1973; Geller and Seifter, 1960; Hanson, Witoslawski, and Campbell, 1967; Hendry and Van Toller, 1964; Morrison, 1969). Recently, however, McMillan and his colleagues (Foree, Moretz, and

Fig. 5. Cumulative records illustrating the effects of *d*-amphetamine on performance maintained by the random-interval schedule and on conditioned suppression. The 3-min preshock stimulus periods are indicated by deflections of the pen. Presentations of reinforcers are not shown. Each record shows performance during a complete session before which a dose of 1 mg/kg was administered, except for R 6 where the dose was 0.5 mg/kg.

McMillan, 1973; McMillan, 1973, 1975) reported experiments in which different temporal patterns of punished responding were

maintained in pigeons and showed that the effects of amphetamines were also rate-dependent in these situations. These results,

Fig. 6. Effects of 1 mg/kg of *d*-amphetamine on responding during successive 30-sec segments of the 3-min pre-shock stimulus. The data were taken from the two or three sessions on which this dose was administered to each animal. X-axis: log of the control response rate. Y-axis: log of the percentage of this control rate observed after administration of the drug. The lines are fitted by the method of least squares.

together with the present ones, emphasize that the actions of amphetamine are dependent on control response rates under a wide variety of experimental conditions.

Our results, therefore, demonstrate the advantages of assessing the actions of a drug on conditioned suppression in terms of a detailed analysis of response rates during the preshock stimulus. The experiment, therefore, suggests that the effects of drugs on behavioral suppression may provide a sensitive technique for use in behavioral pharmacology, though not necessarily allied to motivational interpretations of such disruption that appeal to the effects of drugs on states such as anxiety that cannot be directly observed and measured (Barrett, 1975; Blackman, 1972). The divergent results of previous experiments in which the effects of amphetamines on conditioned suppression have been investigated (Brady, 1956; Cappell *et al.*, 1972; Lauener, 1963; Miczek, 1973) may, to some extent, be related to an insufficiently detailed analysis of the patterns of behavior observed.

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