*EFFECTS OF d-AMPHETAMINE AND
CHLORDIAZEPOXIDE ON SPACED RESPONDING
IN PIGEONS¹*

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The effects of d-amphetamine and chlordiazepoxide were studied in pigeons on performance (1) under a schedule that reinforced responses on a key (food key) if they were more than 20 sec apart, (2) under the same schedule when responses also were required on a collateral key during the interresponse time on the food key, and (3) under the same schedule when responses were required on a collateral key during the interresponse time on the food key and collateral-key responses could produce a stimulus correlated with the availability of food. Under all three spaced-responding schedules, d-amphetamine and chlordiazepoxide at low dose levels slightly increased the frequency of short interresponse times on the food key for about half the birds, and either did not affect the interresponse time patterns of the other birds, or lengthened the durations slightly. At higher dose levels, d-amphetamine and chlordiazepoxide increased the frequency of long interresponse times or abolished responding in all birds. Changes in the pattern of interresponse times on the food key did not seem to depend on changes in the rate or pattern of collateral-key responses.

The differential reinforcement of low rate (DRL) schedule specifies that a response will produce a reinforcer only if it follows the preceding response by more than a specified duration (Ferster and Skinner, 1957). The time periods between consecutive responses under DRL schedules are often analyzed by plotting interresponse time (IRT) frequency distribution histograms. Such IRT frequency distributions have been shown to undergo marked changes when drugs are administered to animals working under DRL schedules, and such schedules frequently have been employed for the study of drug-behavior interactions.

Reports on the effects of amphetamines on performance under DRL schedules have been conflicting. In one of the earliest studies, Sidman (1955) showed in rats that 3 mg/kg dl-amphetamine markedly shifted the IRT distribution toward shorter durations. But more

recently, Hearst and Vane (1967) showed the opposite effect of d-amphetamine in pigeons. They found that over a dose range of 4 to 8 mg/kg, d-amphetamine increased the frequency of long IRTs. In the monkey, Weiss and Laties (1967) reported shifts of the IRT distribution toward both longer and shorter durations.

Conflicting reports on the effects of amphetamine on performance under DRL schedules may depend upon the species studied. Hearst and Vane (1967) studied amphetamine in pigeons, while Sidman (1955) used rats. The notion that pigeons somehow differ from other species in how their performance under DRL schedules is affected by amphetamine is supported by the differences between pigeons and other species in performance under DRL schedules without drugs. For example, Weiss and Laties (1967) show similarly shaped IRT distributions with peaks in the distribution near the minimum IRT that can terminate with the reinforcer, for opossum, rat, monkey, child, man, and raccoon. However, there are many reports that DRL schedules do not exert much control over the IRT distributions of the pecking response of pigeons (Holz, Azrin, and Ulrich, 1963; Reynolds, 1964).

Another difference between pigeon performance and that of other species under DRL

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schedules is that the collateral behavior characteristically seen (Wilson and Keller, 1953) during the IRT is not always obvious in the pigeon (Holz *et al.*, 1963). It has been suggested that collateral behavior mediates the spacing of responses under DRL schedules (Laties, Weiss, Clark, and Reynolds, 1965) and the absence of collateral behavior might explain why there is a lack of control by DRL schedules over pigeon behavior. Further, Segal (1962) suggested that the mechanism by which amphetamine shifts the IRT distribution towards shorter durations in rats is by increasing the rate of collateral behavior (mediating behavior). If pigeons do not exhibit collateral behavior, it would suggest a reason for the difficulty in shifting the IRT frequency distribution toward shorter durations after amphetamine in pigeons.

McMillan (1966*b*) studied a number of variations of a DRL 20-sec schedule in the pigeon. These schedules seemed potentially useful for determining how the amphetamines affect performance under DRL schedules, since they generate a wide range of differences in the spacing of responses under a DRL schedule at a single parameter of the schedule, as well as generating wide ranges in the rates and patterns of collateral behavior.

METHOD

Subjects

Six male White Carneaux pigeons, weighing between 525 and 675 g with free food and water available, were food-deprived to 80% of their free-feeding body weights, and maintained at these weights for the duration of the experiments. Two of the birds had participated in a previous two-key DRL experiment (McMillan, 1969*b*) and the other four birds had several months of exposure to these schedules and other DRL 20-sec schedules before the drug experiments.

Apparatus

The experimental chamber, after Ferster and Skinner (1957), was a sound attenuating chamber. Two translucent, plastic response keys, 0.75 in. (20 mm) in diameter were mounted on an 11 in. (27.5 cm) wide false wall inside the experimental chamber about 3.5 in. (9 cm) apart and 7.75 in. (19 cm) above the chamber floor. One key could be transilluminated with either white or green lamps (col-

lateral key) and the other by red lamps (food key). A feedback relay behind the false wall of the chamber operated whenever 15 g (0.147 N) of force was applied to either key. Centered between the keys about 1.75 in. (4 cm) above the floor was a rectangular opening through which a pigeon could be given 3-sec access to grain. The chamber was illuminated by a 25-w bulb and white noise was always present. Scheduling and recording apparatus were housed in a separate room.

Procedure

Sessions were 30 min in duration. The schedule dependencies are shown in Table 1.

Drugs

The drug forms were d-amphetamine sulfate and chlordiazepoxide hydrochloride, and the dose levels were as the salts. d-Amphetamine was dissolved in physiologic saline, and chlordiazepoxide was dissolved in a "Librium" solvent (1.5% benzyl alcohol, 4% polysorbate 30, 20% propylene glycol, 1.6% malic acid and sodium hydroxide to adjust the pH to approximately 3.0). The solvents alone were used for control injections. All injections were made into the breast muscle in a volume of approximately 0.5 cc about 10 min before a session. Both drugs were studied once at each dose level in every bird under all three DRL schedules. Three birds received a control injection and then an ascending dosage series, while the other three birds received a descending dosage series terminating with the control injection. Birds were tested on Monday through Friday, with drugs or control injections being given on Tuesdays and Thursdays. d-Amphetamine dose-response curves were determined before chlordiazepoxide dose-response curves under each schedule.

Measurement of Drug Effects

IRT frequency distributions in 4-sec class intervals were plotted for the food key after control and drug injections. The rate of responding on the collateral key was determined for each IRT class interval by collecting the number of collateral-key responses in each class interval and dividing this by the number of seconds accumulated on separate elapsed time meters during each class interval. Rates of responding and frequency of food presentation were calculated for entire sessions.

Table 1
Schedule Dependencies and Order of Exposure to Them for Each Bird

Schedule	Food Key Dependency	Collateral Key Dependency ("Sets up" food)	Conditions Producing Stimulus Change on Collateral Key	Order of Exposure to Schedule					
				Bird 7338	Bird 329	Bird 3333	Bird 337	Bird 1556	Bird 7262
Conventional DRL	DRL 20-sec, Red Key	None, key covered	None, key covered	2	3	3	2	1	1
DRL with collateral-key response required	DRL 20-sec, Red Key	One or more responses during food-key IRT	Collateral key always white, no change	1	1	2	3	2	3
DRL with required collateral-key response which could produce a discriminative stimulus	DRL 20-sec, Red Key	One or more responses during food-key IRT	First response on the collateral key after 20-sec IRT on food key changes the color of the collateral key from white to green	3	2	1	1	3	2

RESULTS

Effects of d-Amphetamine on Variations of the DRL 20-Sec Schedule

Figure 1 shows the effects of d-amphetamine on the IRT frequency distributions of selected birds under each variation of the DRL schedule. For the figures, birds were chosen that would be illustrative of trends seen in the group, while at the same time showing some data from every bird. As has been reported (Reynolds, 1964), pigeons do not space their responses far enough apart in time to obtain food very often at these parameters (note control records under the conventional DRL 20-sec schedule).

Under the conventional DRL 20-sec schedule, the highest dose level of d-amphetamine decreased the number of IRTs and shifted the IRT distribution toward long durations. At lower dose levels, two distinct effects were seen. In three of the six birds the IRT frequency distribution shifted toward shorter durations at one of the two lower doses before shifting toward long IRTs at the highest dose. This effect of d-amphetamine is illustrated by the IRT distributions of Bird 337 where a shift toward shorter durations occurs after 0.3 mg/kg d-amphetamine, after which the IRT distribution begins to shift toward longer durations with increasing dosages. Shifts of the IRT distribution toward shorter durations were not observed in the other three birds. The IRT distributions of Bird 329 are illustrative of the effect of d-amphetamine on the performance of the birds whose IRT distributions never shifted toward shorter durations.

Shifting of the IRT distribution toward longer durations after d-amphetamine resulted in more frequent food delivery. This effect is shown in the mean curve for the frequency of food delivery shown in Frame A of Fig. 2. After 3 mg/kg d-amphetamine, the frequency of food delivery more than doubled for the group of birds under the conventional DRL 20-sec schedule, despite the elimination of responding in two birds after 3.0 mg/kg under this schedule.

The middle two columns of Fig. 1 illustrate the effects of d-amphetamine on performance under the DRL 20-sec schedule, where food delivery was dependent upon at least one collateral-key response during the food-key IRT. As previously reported (McMillan, 1969b), pigeons fail to space their food-key responses far enough apart in time to obtain food very often under this schedule (control records of "collateral required" columns in Fig. 1). Not all IRTs greater than 20-sec terminate with food under this schedule. Frame B of Fig. 2 (points above C) shows that after the control injection about half the IRTs longer than 20 sec did not result in food delivery because the birds failed to make a collateral-key response during the food-key IRT.

d-Amphetamine had the same two effects on the IRT distribution under the DRL 20-sec schedule where collateral-key responses were required as it did under the conventional DRL 20-sec schedule. For three of the six birds, the IRT distribution shifted toward shorter durations. These were not necessarily the same birds that showed a similar shift under the conventional DRL schedule. An example of

Fig. 1. Effects of d-amphetamine on patterns of responding of selected birds under three variations of a DRL 20-sec schedule. Abscissa: 4-sec class intervals for IRTs on the food key. Ordinate: left axis (bars) is the frequency of IRTs on the food key during an entire session; right axis (points) is the rate of responding on the collateral key [(response/sec)/class interval]. IRTs shorter than 20 sec are shown by striped bars and IRTs longer than 20 sec are shown by solid bars.

this effect is shown in the IRT distributions of Bird 3333. At 0.3 mg/kg d-amphetamine there were many more IRTs in the first two class intervals, but then at higher dose levels the frequency of short IRTs decreased. The IRT distributions of three other birds shifted toward longer durations without going through the shift toward shorter durations at lower dose levels, as seen in the IRT distributions of Bird 7338.

Although the frequency of IRTs greater than 20 sec almost doubled after 1 mg/kg d-amphetamine, under the DRL schedule that required a collateral-key response during the food-key IRT, the frequency of food delivery did not show a corresponding increase (Frame B, Fig. 2). This is because the rate of responding on the collateral key often decreased fol-

lowing d-amphetamine, thus, many IRTs that were longer than 20 sec did not produce food because no collateral response occurred during the food-key IRT. Covarying decreases in the response rates on the two keys after d-amphetamine can be seen at 0.3 mg/kg and 1.0 mg/kg for Bird 7338 and at 3 mg/kg for Bird 3333 in Fig. 1.

The last two columns of Fig. 1 show the effects of d-amphetamine on the rate of collateral-key responding and on the food-key IRT distribution under the DRL schedule where collateral-key responses not only were required during the food-key IRT, but also, collateral-key responses could produce a stimulus (change in the color of the collateral key) correlated with availability of food under the DRL 20-sec schedule. As previously reported

Fig. 2. Total number of IRTs longer than 20 sec in a session (filled circles and solid lines) and number of these IRTs longer than 20 sec that produced food (open circles and broken lines). Each point is the mean of single observations in each of six birds. Points above C in each frame show data during injection control sessions.

for pigeons (McMillan, 1969b), this schedule generates a fixed-interval pattern of collateral-key responding (a pause followed by an increasing response rate) and a higher frequency of food delivery than do the other two DRL

schedules (compare "collateral-produced cue" columns with other columns in Fig. 1). Injections of d-amphetamine had very small effects on the IRT distributions under this schedule until high dose levels stopped key pecking almost entirely. Nevertheless, after low doses of the d-amphetamine the IRT distributions of at least two birds showed a small tendency toward an increased frequency of short durations. The IRT distributions of one of these birds (Bird 7262) is shown in Fig. 1. Note the increased frequency of short IRTs in the first class interval after 0.3 mg/kg d-amphetamine. Other birds, as shown in the IRT distributions of Bird 1556, did not show any increase in short IRTs before responding was slowed or eliminated. Thus, the effect of d-amphetamine on the IRT distribution was in the same direction under all three variations of the DRL schedule.

Under the DRL schedule where collateral-key responses could produce a discriminative stimulus, most IRTs were between 20 and 24 sec after control injections (Fig. 1) and produced food (Frame C, Fig. 2). Shifts in the IRT distribution toward either long or short IRTs decreased the total number of IRTs greater than 20 sec and reduced the frequency of food delivery, since control performance came close to maximizing the frequency of food delivery. Decreases in the number of IRTs greater than 20 sec and in the frequency of food delivery as a function of increasing d-amphetamine dosage are shown for this schedule in Frame C of Fig. 2.

The color change on the collateral key functioned as a conditioned reinforcer to maintain a fixed-interval pattern of collateral-key responding. However, d-amphetamine did not increase the rate of collateral-key responding very much. In three birds there was only a 5 to 10% increase in the rate of collateral-key responding (e.g., Bird 7262 in Fig. 1) and in the other three birds there was no increase in the rate of collateral-key responding. At the same dose levels investigated in this study, d-amphetamine markedly increased rates of responding under fixed-interval schedules of food presentation (e.g., McMillan, 1968).

Effects of Chlordiazepoxide on Variations of the DRL 20-Sec Schedule

The effects of chlordiazepoxide on the IRT frequency distributions under the three variations of the DRL 20-sec schedule are shown

in Fig. 3. Chlordiazepoxide had effects on performance under the conventional DRL schedule similar to those of d-amphetamine. Three of the birds showed shifts of the IRT frequency distribution toward shorter durations at either 1 or 3 mg/kg chlordiazepoxide (illustrated by Bird 329), before the frequency of long IRTs increased at higher dose levels. The other three birds never showed an increased frequency of short IRTs before the frequency of long IRTs increased (illustrated by Bird 337). As with d-amphetamine, the same birds did not necessarily show the same type of shift in the IRT distribution under all three schedule variations. Since the frequency of IRTs longer than 20 sec increased after 3 mg/kg chlordiazepoxide for some birds, Frame D of Fig. 2 shows that food was delivered more frequently after this dose level. However, most

birds were responding infrequently after 10 mg/kg chlordiazepoxide, therefore, the frequency of food delivery decreased. Chlordiazepoxide, at low doses, increased the frequency of short IRTs for three birds under the DRL 20-sec schedule requiring a collateral-key response (illustrated by Bird 7262 in Fig. 3). At higher doses the frequency of long IRTs increased or responding was abolished. The other three birds showed only an increase in the frequency of long IRTs or suppression of responding (e.g., Bird 7338). These effects also were very similar to those of d-amphetamine. Frame E of Fig. 2 shows that 1 mg/kg and 10 mg/kg chlordiazepoxide decreased the frequency of food delivery. The 1 mg/kg decrease in food delivery resulted from the shift in the IRT distribution toward shorter dura-

Fig. 3. Effects of chlordiazepoxide on patterns of responding of selected birds under three variations of a DRL 20-sec schedule. Abscissa: 4-sec class intervals for IRTs on the food key. Ordinate: left axis (bars) is the frequency of IRTs on the food key during an entire session; right axis (points) is the rate of responding on the collateral-key [(responses/sec)/class interval]. IRTs shorter than 20 sec are shown by striped bars, and IRTs longer than 20 sec are shown by solid bars.

tions (few changes in the rates of collateral key responding were observed at 3 mg/kg), while the 10 mg/kg decrease was primarily a function of the elimination of food-key responding.

As with d-amphetamine, chlordiazepoxide did not have marked effects on the IRT distributions under the DRL 20-sec schedule where collateral-key responses produced a discriminative stimulus for food-key responding. Nevertheless, chlordiazepoxide, like d-amphetamine, caused slight increases in the frequency of short IRTs of some birds (*e.g.*, Bird 3333 in Fig. 3), while the other birds (illustrated by Bird 1556 in Fig. 3) did not show this effect. At higher dose levels there was an increased frequency of long IRTs or an elimination of responding for all six birds.

Since most food-key IRTs were between 20 and 24 sec after the control injections, all changes in the IRT distributions necessarily resulted in a decreased frequency of IRTs in this class interval, which in turn resulted in a decreased frequency of food delivery. Under both drug and control conditions the frequency of food delivery closely approximated the frequency of IRTs between 20 and 24 sec (Frame F of Fig. 2).

At some dose level, chlordiazepoxide increased the rate of collateral-key responding of every bird except one, under the schedule where collateral-key responses produced the discriminative stimulus for food-key responding. The size of the rate increase varied from 9 to 59% of the control rate of responding. For three birds the increased collateral-key rate was maintained over two dose levels.

DISCUSSION

The most obvious effect of d-amphetamine on performance under the conventional DRL 20-sec schedule was to increase the long IRT durations or to eliminate responding at the higher dose levels. Since the control performance was marked by a preponderance of short IRTs, the increase in the frequency of long IRTs resulted in food being presented more frequently after the higher dose levels. These results are in agreement with those of Hearst and Vane (1967). However, the small tendency toward an increased frequency of short IRTs seen in some birds after low dose levels of d-amphetamine is similar to the effects of am-

phetamine in rats (Sidman, 1955). Thus, d-amphetamine in pigeons produces shifts in the IRT distribution toward both longer and shorter durations.

Possibly, d-amphetamine in pigeons increased the frequency of long IRTs under the DRL schedules by increasing the frequency of food delivery. If d-amphetamine induced occasional pauses in responding, termination of the pause would produce the reinforcer. Since most birds rarely produced the reinforcer, increases in the frequency of food delivery after d-amphetamine might reinforce subsequent pauses. However, the effects of d-amphetamine on behavior under the schedule requiring collateral-key responses argues against this mechanism. Under this schedule, the frequency of food delivery was lower than the frequency of IRTs greater than 20 sec, because many IRTs greater than 20 sec were not accompanied by collateral-key responses. When 1 mg/kg d-amphetamine was given, the number of IRTs longer than 20 sec increased markedly; however, the frequency of food delivery did not show a corresponding increase because the rate of responding on the collateral-key usually decreased. Thus, d-amphetamine increased the frequency of long IRTs even though the frequency of food delivery did not increase.

Under the schedule requiring collateral-key responses, d-amphetamine usually decreased the rate of collateral-key responding, but there was no consistent relationship between changes in the rate of collateral-key responding and changes in the pattern of food-key responding. Thus, it is unlikely that the effects of d-amphetamine on the spacing of food-key responses were mediated through changes in the pattern of collateral-key responses.

Although relatively high rates of collateral-key responding were maintained in a fixed-interval pattern under the schedule where collateral-key responses produced a discriminative stimulus, they did not change systematically with the pattern of food-key responding after d-amphetamine. That the rate of collateral-key responding increased only slightly after d-amphetamine was unexpected, since responding on the collateral-key to produce the change in key-light color is a chain schedule (Ferster and Skinner, 1957) and chain schedules are susceptible to the rate-increasing effects of drugs (*e.g.*, Thomas, 1965).

The failure of d-amphetamine to increase collateral-key responding may be related to the very short fixed-interval duration (about 20 sec). McMillan (1969a) has shown that responding does not increase much after amphetamine when fixed-interval schedules of 60 sec maintain the behavior.

It was very difficult to differentiate the effects of d-amphetamine from those of chlor-diazepoxide. Both drugs had only small effects on the IRT distributions at dose levels that did not abolish responding and both drugs had small effects on the rate of collateral-key responding.

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