EFFECTS OF *d*-AMPHETAMINE AND CAFFEINE ON SCHEDULE-CONTROLLED AND SCHEDULE- INDUCED RESPONDING

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The effects of *d*-amphetamine and caffeine were studied on rates and patterns of lever pressing and schedule-induced licking under fixed-interval schedules of food pellet presentation. In addition, the effects of caffeine were studied on lever pressing and licking under a multiple fixed-ratio fixed-interval schedule. Caffeine reduced mean overall rates of licking at lower doses than it reduced mean overall rates of pressing under the fixed-interval schedules, but the effects of caffeine on both licking and lever pressing depended largely on the control rate of responding. *d*-Amphetamine reduced mean overall rates of lever pressing and licking at about the same dose, but the effects of *d*-amphetamine also were a function of the control rate of responding.

Key words: fixed-interval schedule, schedule-induced licking, rate dependency, *d*-amphetamine and caffeine, rats

The effects of *d*-amphetamine on schedule-controlled behavior and drug self-administration are well known. For example, *d*-amphetamine decreases the high rates of responding generated by fixed-ratio schedules (Dews & Wenger, 1977; McMillan, 1968a; Smith, 1964) and increases the low rates of responding generated by fixed-interval schedules (McMillan, 1969; Smith, 1964), especially those rates at the beginning of the fixed interval. Furthermore, *d*-amphetamine (Balster & Schuster, 1973; Pickens & Harris, 1968) maintains intravenous self-administration in a variety of species.

In contrast, considerably less is known about the effects of caffeine on schedule-controlled behavior and self-administration, despite its widespread use in human beings. Caffeine increases the low rates of responding generated by fixed-interval schedules in pigeons and monkeys (Davis, Kensler & Dews, 1973; McMillan, 1968b); however, in pigeons, low rates of responding under fixed-interval schedules are decreased at lower doses than the higher rates under FR schedules (McMillan, 1968b).

The purpose of the present experiment was to compare the effects of *d*-amphetamine and

caffeine under some schedules that generate schedule induced polydipsia (Falk, 1961). These experiments on the effects of injections of these drugs were done as a prelude to studying their oral self-administration under schedule-induced polydipsia.

METHOD

Subjects

Twelve male Sprague-Dawley rats approximately 120 days of age at the start of the experiments were used. Four of the rats were used to study the effects of *d*-amphetamine on fixed-interval responding (R1, R2, R3, R4), four rats were used to study the effects of caffeine on fixed-interval responding (R9, R10, R11, R12), and four rats were used to study the effects of caffeine on multiple fixed-interval fixed-ratio responding (R5, R6, R7, R8). The rats used to study the effects of *d*-amphetamine on fixed-interval responding also received injections of what was thought to be cocaine but it was later discovered that this sample contained impurities such as procaine, and so the data were discarded. The rats were food deprived for 48 hr and maintained at the resulting weights (245 to 285 g) throughout the experiments by food pellet deliveries during the test sessions and by postsession supplemental feedings. Tap water was always available in each rat's home cage.

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Apparatus

The experimental chamber was a rat test cage (Lehigh Valley Electronics) housed within a sound-attenuating chamber. Rat pellets (Noyes, 97 mg) could be dispensed into a receptacle in the middle of the stimulus panel of the test cage. A rat lever (Gerbrands) requiring 30 g of force to operate was situated 5.5 cm to the right of the food receptacle and 4.2 cm off the grid floor. A 1-cm hole above the lever (10 cm off the floor) allowed access to the drinking tube of the water bottle. The drinking tube was recessed 1 cm behind the stimulus panel. Licks on the drinking tube were recorded with a drinkometer (Grason-Stadler). Licks and lever presses were recorded on cumulative recorders and digital counters. The water bottle was weighed before and after each session to determine the amount of solution ingested (assuming 1 ml of solution = 1 g) with a 1 ml correction for spillage and evaporation (obtained by placing water bottles on the cage for 75 min without a rat in the test chamber).

Procedure

The eight rats used to study the effects of *d*-amphetamine (R1, R2, R3, R4), or caffeine (R9, R10, R11, R12) on fixed-interval responding were trained to lever press by successive approximations during an initial session. Subsequently, responding was maintained under a fixed-interval 90-sec schedule (FI 90) of food presentation (the first lever press after 90 sec produced food). Sessions were 75 min in duration and were conducted Monday through Friday. After approximately 20 sessions under FI 90, dose-effect curves were determined for intraperitoneal injections of the procaine-cocaine mixture (not reported), *d*-amphetamine (.1 to 3.0 mg/kg), or caffeine (10 to 100 mg/kg). Drug or control injections, in a volume of 1 ml/kg of body weight, were given on Tuesdays and Fridays, 1 min before the start of the session. Thursdays served as a noninjection control session. Data from Mondays and Wednesdays were not analyzed. Half of the rats received each drug in an ascending dosage series (R1, R2, R9, R10) with the first injection in the series being a control injection, and half of the rats received each drug in a descending dosage series (R3, R4, R11, R12) with the last injection in the series being a control in-

jection. The four rats studied with *d*-amphetamine had received the procaine-cocaine mixture first.

The four rats used to study the effects of caffeine (R5, R6, R7, R8) on multiple fixed-ratio fixed-interval responding were trained to lever press by successive approximations during an initial session. Then responding was maintained under a multiple fixed-ratio 10-response (FR 10) fixed-interval 90-sec (FI 90) schedule of food presentation. If the rat did not make 10 responses within the 1-min period of tone, which was on only during the fixed-ratio component, the schedule changed to the fixed-interval component. If the rat did not respond within a 1-min period after the fixed-interval 90-sec period had elapsed, the schedule changed to the FR component. Schedule components alternated with food delivery, or expiration of the 1-min periods. Sessions were 75 min in duration and were conducted Monday through Friday. After approximately 30 sessions under the multiple schedule, dose-effect curves were determined for intraperitoneal injections of caffeine (10 to 100 mg/kg). The drug was administered in a volume of 1 ml/kg of body weight on Tuesdays and Fridays, 1 min before the beginning of the session. Thursdays served as noninjection control sessions. Data from Mondays and Wednesdays were not analyzed. Two rats (R5 and R6) received caffeine in an ascending dosage series with the first injection in the series being a control injection, and two rats (R7 and R8) received caffeine in a descending dosage series with the last injection in the series being a control injection. Injections were given 1 min before the beginning of the session. Each rat received each dose of caffeine twice.

Drugs

Drug doses were calculated as the salts. Caffeine was given as the sodium-benzoate and *d*-amphetamine as the sulfate.

RESULTS

Patterns of Fixed-Interval Responding

The fixed-interval schedule generated two distinct patterns of lever pressing and licking of the drinking tube. One pattern, similar to that described previously by McKearney (1973) and by McMillan and Leander (1976), was seen in five of the eight rats. This pattern was

Fig. 1. Patterns of licking and lever pressing under the fixed-interval schedule by rats under control conditions. The pen steps upward following each lick on the drinking spout. Downward deflections on the pen show lever presses. The pen resets to baseline upon delivery of food.

characterized by pellet delivery followed by a sustained high rate-licking episode, followed by a short pause, which in turn was followed by a gradually increasing rate of responding on the lever. These effects can be seen for Rats R1 and R3 in Figure 1, where upward travel of the pen shows licks and downward deflection marks show lever presses.

The pattern of lever pressing and licking was different in the other three rats. Because

the hole to the licking tube was directly above the lever, it was possible for these rats to lever press and lick simultaneously and they often did. Pellet delivery was followed by a high rate of licking accompanied by occasional lever presses. This was followed by a gradually increasing rate of lever pressing, but licking also occurred late in the fixed interval. Examples of these effects can be seen in Rats R2 and R4 in Figure 1.

Acute Effects of *d*-Amphetamine and Caffeine on Patterns of Fixed-Interval Responding

Figure 2 shows the effects of *d*-amphetamine on mean rates of lever pressing (top frame),

Fig. 2. Effects of *d*-amphetamine injections on lever pressing, licking, and volume of water consumed. The brackets at CONTROL show the range of values during 8 noninjection sessions (Thursdays) for each rat and the points at CONTROL show the effects of a vehicle injection. Numbers at CONTROL and beside the dose-effect curves are identification numbers for individual rats. Each point on the dose-effect curve is a single observation for each rat.

licking (middle frame), and volume consumed (bottom frame) averaged over the entire session for Rats R1, R2, R3, and R4. Doses of .1 to 1.0 mg/kg did not produce reliable effects across animals, whereas the 3.0 mg/kg dose decreased the rate of lever pressing of all rats except for Rat R1. Generally, the rate of licking was decreased by the same doses of *d*-amphetamine that decreased the rate of lever pressing, except that 3.0 mg/kg decreased the licking rate of Rat R1 but not the rate of lever pressing. Changes in the volume consumed were similar to changes in the licking rate.

Figure 3 shows the effects of caffeine on mean rates of lever pressing (top frame), licking (middle frame), and volume consumed (bottom frame) averaged over the entire session for Rats R9, R10, R11, and R12. Rats R9 and R10 had higher baseline rates of lever pressing, which were decreased only after 100 mg/kg caffeine. Rats R11 and R12 had lower rates of lever pressing which were not decreased by any of the doses of caffeine that were studied.

Rates of licking were decreased by caffeine at lower doses than were rates of lever pressing. For example, in Rats R11 and R12, 100 mg/kg caffeine decreased rates of licking but not rates of lever pressing. For Rat R9, a dose of 10 mg/kg caffeine reduced the licking rate, but 56 mg/kg was required to reduce the rate of lever pressing. For Rat R10, rates of licking were decreased by 30 mg/kg caffeine, but 100 mg/kg was required to decrease lever pressing. In general, changes in the volume consumed were similar to the licking rate data.

The effects of the two highest doses of *d*-amphetamine on rates of lever pressing and licking during consecutive 18-sec segments of the fixed interval are shown in Figure 4. Relative to performance after the control injection (C), 1.0 mg/kg *d*-amphetamine had little effect on lever pressing. By comparison, the 3.0 mg/kg dose produced rate-dependent effects in all four rats. The lowest control rates of lever pressing, which occurred in the first or second class interval (0 to 36 sec after the beginning of the fixed interval) were increased and higher rates during the last two class intervals (54 to 90 sec after the beginning of the fixed interval) were decreased. *d*-Amphetamine had less consistent effects on local rates of licking. The

Fig. 3. Effects of caffeine injections on lever pressing, licking, and volume of water consumed. The brackets show the range of values during 7 noninjection sessions (Thursdays) for each rat and the points at CONTROL show the effects of a vehicle injection. Numbers at CONTROL and beside the dose-effect curves are identification numbers for individual rats. Individual dose-effect curves are plotted for each rat.

high rates at the beginning of the fixed interval were decreased (3.0 mg/kg) or unaffected (1.0 mg/kg) but both increases and decreases in licking rates were observed at the end of the interval.

The effects of the two highest doses of caffeine on local rates of lever pressing and licking are shown in Figure 5. In Rats R9 and

R10, 100 mg/kg generally decreased rates of responding, but this dose of caffeine in Rats R11 and R12, as well as 56 mg/kg caffeine in all rats, tended to increase low rates of responding in the middle of the fixed interval (class interval 2 for R9 and class intervals 3 and 4 for the other rats). The 100 mg/kg dose of caffeine nearly eliminated licking by Rats R9 and R10, but this dose increased the low rate of licking in the last two class intervals by R11 and R12.

In summary, caffeine decreased licking rates under the fixed-interval schedule at lower doses than it decreased rates of lever pressing, but for *d*-amphetamine the same doses usually decreased lever pressing and licking. Both drugs increased low rates of lever pressing during the earlier parts of the fixed interval, but increases during class intervals 2 and 3 (18 to 54 sec) were frequently greater than increases during the first class interval (0 to 18 sec). Both drugs decreased high rates of licking at the beginning of the interval. Both increases and decreases in rates of licking occurred at the end of the fixed interval with these drugs, but the rate increases were more likely to occur if the control rates were low (less than 0.1 responses/sec).

Patterns of Multiple Fixed-Interval Fixed-Ratio Responding

As with the simple fixed-interval schedule, the fixed-interval component of the multiple schedule generated positively accelerated patterns of lever pressing in Rats R5, R6, R7, and R8, although R6 and R8 showed higher rates during the first class interval than the second class interval. All four rats showed the usual sustained high rate licking episode at the beginning of the fixed-interval component immediately after food pellet delivery under the fixed-ratio component. For three of the four rats, licking was maintained, although at a lower rate, late in the interval (the record for R6 in Figure 6 is an example of this pattern of lever pressing and licking). The remaining rat (R5) licked very little near the end of the interval. Cumulative records illustrating control performance of two subjects are shown in Figure 6. The top record for each rat shows lever pressing and the second row shows the pattern of licking. Rat R5 licked at the beginning of

Fig. 4. Effects of *d*-amphetamine on patterns of licking and lever pressing during the fixed interval. The ordinate is a log scale for rate of responding and the abscissa shows the successive 18-sec class intervals into which the fixed interval was divided. Responses have been cumulated throughout a session for each segment of the fixed interval and then plotted as an average rate of responding for each rat. The C in the upper frame is for the vehicle injection (●—●), and the 1.0 (▲---▲) and 3.0 (□—□) are mg/kg doses of *d*-amphetamine. Each point is an average rate for a class interval for the entire session.

the fixed interval and lever pressed at the end, whereas Rat R6 did both licking and lever pressing late in the interval.

Rates of lever pressing were slightly higher for all rats during the fixed-ratio component of the multiple schedule than during the fixed-

Fig. 5. Effects of caffeine on patterns of licking and lever pressing during the fixed intervals. The ordinate is a log scale for rate of responding and the abscissa shows the successive 18-sec intervals into which the fixed-interval was divided. Responses have been cumulated throughout a session for each segment of the fixed interval and then plotted as an average rate of responding for each rat. The C in the upper left frame of Rat 9 is for the vehicle injection (●—●), and the 56 (▲---▲) and 100 (□—□) are mg/kg doses of caffeine.

Fig. 6. Patterns of lever pressing and licking under the multiple fixed-ratio fixed-interval schedule for Rat R5 and Rat R6 under control conditions. The pen stepped upward following a lever press (frames 1 and 3) or a lick (frame 2 and 4). Deflections on the lever pressing records show food delivery. Pen offsets on the horizontal line under the licking records show time spent in the fixed-interval component (pen up) and the fixed-ratio component (pen down).

interval component, as can be seen by comparing control performance under the fixed-interval component (Figure 7) with those under the fixed-ratio component (Figure 8). Generally, once fixed-ratio responding was initiated, it continued at a high rate. For two rats (R6 and R8), high rates of licking occurred

Fig. 7. Effects of caffeine on volume consumed on lever pressing and licking under the multiple fixed-interval fixed-ratio schedule. The brackets at CONTROL show the range of values during 6 noninjection sessions for each rat, and the points at CONTROL show the effects of a vehicle injection. Numbers at CONTROL and beside the dose-effect curves are identification numbers for individual rats. Each point represents two observations on each animal.

after pellet delivery under the fixed-interval schedule before lever pressing during the fixed-ratio component was initiated. The other two rats did very little licking during the fixed-ratio component. The rats with the high licking rates during the fixed-ratio component tended to have low rates of lever pressing.

Fig. 8. Effects of caffeine on rates of lever pressing and licking under the fixed-ratio component of the multiple fixed-interval fixed-ratio schedule. The brackets at CONTROL show the range of values during 6 noninjection sessions for each rat, and the points at CONTROL and beside the dose-effect curves are identification numbers for the same rats shown in Figure 7. Each point represents two observations in each animal.

Acute Effects of Caffeine on Patterns of Responding under the Multiple Schedule

The effects of caffeine on mean rates of lever pressing (top frame), licking (middle frame), and volume consumed (bottom frame) during the fixed-interval component of the multiple schedule are shown in Figure 7. Doses as high as 100 mg/kg produced little effect on lever pressing; however, the 100 mg/kg dose of caffeine decreased the rate of licking and the volume of water consumed by all rats, and lower doses of caffeine produced similar but smaller decreases in some rats.

The effects of caffeine on lever pressing and licking are shown in Figure 8 for the fixed-ratio component of the multiple schedule. Rat R8 showed an increase in the rate of lever pressing after the 30 mg/kg dose (top frame), but this was the only instance of a rate-increasing effect on lever pressing under the ratio schedule. In general, the highest doses decreased rates of lever pressing, except for rat R7.

The effects of caffeine on licking during the fixed-ratio component depended on whether the animals licked at a high rate or a low rate during that component. Rats R6 and R8 (middle frame) licked at a high rate during the fixed-ratio component and showed only dose-related decreases in rates of licking. Rats R5 and R7 (bottom frame) licked at a low rate during the fixed-ratio component, and caffeine produced increases in licking rate during that FR component, especially after the 56 mg/kg dose. Thus, licking during the fixed-ratio component was rate dependent—the rats with high licking rates showed decreases in licking after caffeine and those with low rates showed rate increases.

Figure 9 shows the effects of caffeine on local rates of responding within the fixed-interval (left column). Caffeine frequently increased low rates of lever pressing during the second and third 18-sec segments of the fixed interval. Rates of lever pressing at the beginning and end of the interval were little affected, except for Rat R7, who showed rate increases in the middle of the interval and rate decreases at the beginning and end.

The right column of Figure 9 shows the effects of caffeine on local rates of licking within the fixed-interval component. For Rats R5, R7, and R8, the high rates of licking at the beginning of the interval were decreased by caffeine; for Rat R6, caffeine had little effect. The two rats with the lowest rates of licking at the end of the fixed interval (R5 and R8) showed rate increases after caffeine, whereas those with higher rates of licking at the end of the fixed interval (R6 and R7), showed decreases.

DISCUSSION

Amphetamines (McKearney, 1973; Sanger, 1977a, b; Segal & Deadwyler, 1964; Smith & Clark, 1975), benzodiazepines (Barrett & Weinberg, 1975; Sanger, 1977a; Sanger & Blackman,

CAFFEINE

Fig. 9. Effects of caffeine on patterns of licking and lever pressing during the fixed-interval component of the multiple fixed-interval fixed-ratio schedule. The ordinate is a log scale for rate of responding and the abscissa shows successive 18-sec intervals into which the fixed interval was divided. The solid points are for control injections, the open triangles for 56 mg/kg doses of caffeine and the open squares for 100 mg/kg doses. Each point is an average rate for class intervals from two sessions.

1976; Smith & Clark, 1975), and haloperidol (Keehn, Coulson, & Klieb, 1976) have all been shown to affect schedule-induced drinking. Although fixed-time schedules were used to generate polydipsia in some of these experiments, in others food was delivered as a consequence of lever pressing, and it was recognized that drugs could affect schedule-controlled lever pressing and schedule-induced polydipsia differently (Segal & Deadwyler, 1964). Such differences in drug effects might depend on different response topographies (lever pressing versus licking), different maintaining events (schedule control versus schedule induction), different degrees of behavioral control (Smith & Clark, 1975), differences in rates of behavior (licking usually occurs at much higher rates than lever pressing), or other variables. The use of behavioral pharmacology to analyze differences between schedule-controlled and schedule-induced behavior already has been suggested (Smith & Clark, 1975).

In the present experiments, the spatial proximity of the lever and drinking spout allowed a variety of patterns of lever pressing and licking to occur, which provided distinctive baseline patterns of responding for the analyses of drug-behavior interactions. For example, analysis of rates of responding during successive 18-sec segments of the fixed-interval schedule permitted the analysis of lever pressing rates from near zero to in excess of 1 response/sec and licking rates of from near zero to even higher rates than 1 response/sec. These baseline rates during the fixed interval coupled with varying rates of responding during the fixed-ratio component of the multiple schedule provided a wide range of rates of both licking and lever pressing against which to evaluate the effects of drugs.

Perhaps the most important finding in these experiments was that the effects of *d*-amphetamine and caffeine on both lever pressing and licking depended on the control rate of responding. The high rates of licking that occurred during the first few class intervals of the fixed-interval schedule, or the high rates of licking that was produced by some rats (R6 and R8 in Figure 10) during the fixed-ratio component of the multiple schedule, were only decreased by both of these drugs. When licking was well maintained late in the fixed interval, it was usually decreased by these drugs. Similarly, the high rates of lever pressing that

occurred late in the fixed interval also were decreased by these drugs as has been reported previously (McMillan, 1968a, b; McMillan, Dearstyne, and Engstrom, 1975; Smith, 1964). In contrast, the low rates of licking that occurred late in the fixed interval for some of the rats and that occurred during the fixed-ratio component for Rats R5 and R7 were increased by these drugs. Similarly, low rates of lever pressing that occurred during the first two or three class intervals of the fixed interval were frequently increased by these drugs, again as has been reported previously (McMillan, 1968a, b; McMillan et al., 1975; Smith, 1964). Thus, regardless of the topography of the response (licking or lever pressing) or the nature of the maintaining events (reinforcement of lever presses, schedule-induction of licking and possibly adventitious reinforcement of licking late in the fixed interval), the effects of the drugs could be described as being rate dependent. Under these conditions, the control rate of responding appears to be a more powerful determinant of the effects of CNS stimulants than the response topography or the events that maintain responding.

If the effects of these drugs depend on the control rate of responding, why did caffeine reduce mean overall rates of licking at lower doses than those that reduced rates of lever pressing while *d*-amphetamine reduced licking and lever pressing at approximately the same dose level? The answer to this question may be that, although the effects of both drugs were rate dependent, there remain differences in the behavioral pharmacology of these drugs. Whether these differences simply represent subtle differences in the rate dependency or are a function of other factors, such as differences in the response topographies or the events maintaining lever pressing and licking, cannot be determined on the basis of these experiments.

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