

Drugs and the Discrimination of Duration

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Abstract. The effects of lysergic acid diethylamide (LSD), *d*-amphetamine (AMP), chlorpromazine (CPZ), and the most active isomer of marihuana (Δ^9 -THC) on timing behavior were analyzed with a two-choice, discrete trial procedure in which pigeons were trained to discriminate visual stimuli that differed with respect to duration ('long' vs. 'short'). LSD (0.01, 0.04, 0.16 mg/kg) decreased response speed (increased latency), but otherwise had no significant effects on performance of the discrimination. *d*-Amphetamine (1.0, 2.0, 4.0 mg/kg) increased perseveration or 'spatial bias' and, at a dose of 4.0 mg/kg, lowered response speed. This compound did not significantly alter accuracy (percentage correct). CPZ (7.5, 15.0, 30.0 mg/kg) significantly decreased accuracy and, at a dose of 30.0 mg/kg, significantly lowered speed; THC also decreased accuracy and lowered speed. Neither CPZ nor THC significantly altered perseveration.

Key words: LSD – *d*-Amphetamine – Chlorpromazine – THC – Temporal discrimination – Timing – Latency – Birds

A large and increasing body of literature describes abnormalities and distortions in the perception of time induced by psychoactive drugs in human subjects. Indeed, this literature suggests that it is rare for subjective time to remain 'normal' following ingestion of such drugs as lysergic acid diethylamide (LSD). Hoffer and Osmond (1967), for instance, report that "subjective awareness of time passing was altered in most subjects. It stopped, slowed up or speeded up and even ran backward" (p. 119).

The question of whether or not similar drug-induced alterations in time perception occur in lower animals is difficult to answer. While it is clear that many, if not all, psychoactive drugs can increase (facilitate) or decrease (depress) the rate of responding under the control of time-based schedules of reinforcement (e.g., fixed-interval), it is much less clear that these effects necessarily involve timing. Rather, patterns of schedule-controlled behavior (and their disruption by drugs) can be explained more parsimoniously in terms of schedule 'dynamics,' i.e., without reference to any internal timing mechanism (Catania, 1970; Dews, 1970; Altman and Appel, 1975). It is only when a response becomes more likely after a stimulus of one duration than after another that a temporal discrimination is clearly evident (Catania, 1970), and only when such a discrimination has been established can we conclude unequivocally that a given drug affects the perception or 'sense' of time (i.e., duration).

Unfortunately, there have been only a few studies on the discrimination of stimulus duration by lower animals (Woodrow, 1928; Cowles and Finan, 1941; Heron, 1949; Reynolds and Catania, 1962; Stubbs, 1968; Catania, 1970) and even fewer studies concerned with the influence of drugs on such discrimination (Dykstra and Appel, 1974; Stubbs and Thomas, 1974; Rapp and Robbins, 1976). Amphetamine (i.e., *d*-amphetamine sulfate) has been reported to decrease the ability of both rats (Rapp and Robbins, 1976) and pigeons (Stubbs and Thomas, 1974) to discriminate among temporally defined stimulus differences.

LSD had little effect on a similar task in rats (Dykstra and Appel, 1974) and pigeons (Straub and Appel, 1975), but it did produce a significant decrease in sensitivity in squirrel monkeys (Dykstra, 1972). In all of these experiments, both compounds increased perseverative responding (spatial biases) and response latencies.

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The present investigation is concerned with the effects of *d*-amphetamine (AMP), chlorpromazine (CPZ), and Δ^9 -tetrahydrocannabinol (THC) on the discrimination of duration in the pigeon. These compounds were chosen because each has been implicated in reports of perceptual distortions in humans (Barber, 1970) and because much is known about their behavioral effects in lower animals. The experiment was designed to determine whether drug-induced changes in the organism's sensitivity or accuracy to stimulus duration (that is, in its 'sense of time') occurred and the extent to which these changes were accompanied by changes in response perseveration or spatial bias.

Materials and Methods

Subjects. Four male, white, Carneaux pigeons (obtained from the Palmetto Pigeon Plant, Sumter, South Carolina) were maintained with food and water continuously available for 3 months, and a free-feeding weight was obtained for each bird. The pigeons were then reduced to 80% of their free-feeding weights and kept at that level by varying the amount of food mixture (40% vetch, 50% Kaffir corn, 10% hemp seed) they received during the experimental sessions. The four birds were approximately 2 years old and, except for two that had previously participated in a 'match to sample' study, were experimentally naive. Water was always available in home cages, which were housed in a room of constant temperature (22° C) and humidity (40–50%) with a 12-h-light-dark cycle (7:00 a.m. – 7:00 p.m.).

Apparatus. The experimental box was a commercially manufactured three-key pigeon chamber (BRS/LVE Model 132-02). Each key could be illuminated by any one of a series of 12 IEE visual patterns. In addition, two, dim 7-W house lights illuminated the chamber during the session. White noise was generated in the box to mask the sounds of external stimuli.

Contingencies were programmed automatically by relay and timing circuits located in an adjoining room. Counters recorded correct, incorrect, and premature responses (responses that occurred during the presentation of the discriminative stimulus) while a running time meter recorded the time between successive trials (end of trial t-1 or beginning of the session – until the center key response on trial t).

Behavioral Procedure. The pigeons were trained to respond differentially to two temporal stimuli, 4.5 and 5.5 s in duration, by selecting the correct side key. Each day, the pigeon was removed from its home cage, weighed, and placed in the completely dark experimental chamber. At the beginning of the session, the house lights were turned on and remained on throughout the session, except for the 10-s time-out periods that occurred when the pigeon responded either prematurely or incorrectly. The session consisted of 300 trials, each of which began with the center key illuminated by a 1.3-cm diameter white circle and with the two side keys dark. A single peck on the center key (the initiating response) turned off the white circle and initiated the temporal stimulus: a 0.64-cm diameter red circle on the center key for either 4.5 s ('short') or 5.5 s ('long'). Short and long stimuli alternated randomly with the restriction that each stimulus occur on 50% of the trials during each session (150 trials) and that the same stimulus could not occur on more than three successive trials. At the end of the temporal stimulus, the red light was extinguished and, simultaneously, both side keys were illuminated by 1.3-cm diameter white circles. A correct response sequence consisted of pecking the right side key after the presentation of the short temporal stimulus or pecking

the left side key after the long stimulus. Correct sequences were followed by conditioned reinforcers consisting of a 1.3-s presentation of a light above the food hopper (feeder-flash) and, on certain trials, by grain. The length of the reinforcement cycle was inversely related to the weight of each pigeon (birds low in weight were permitted longer access to the hopper) so that each bird was maintained at 80% of its free-feeding weight from the food it received during the experimental sessions and required no supplementary feeding. Incorrect response sequences (pecking the left key after the presentation of the short stimulus or the right key after the long stimulus) were followed by a time-out of 10 s (TO 10), during which all chamber lights were extinguished and responding (on any of the keys) had no consequences. Time-outs also occurred if any key was pecked during the temporal stimulus, since there was some indication that birds have difficulty withholding responding to illuminated keys (Schwartz and Williams, 1971) and there is evidence that responses during stimulus presentation interfere with the accuracy of the discrimination (Stubbs, 1968). With the termination of the time-out period, the feeder-flash, or the reinforcement cycle, the center key was again illuminated by the white light, and the next trial began.

The frequency of food reinforcement following either left or right correct sequences was varied independently so that either symmetrical or asymmetrical probabilities occurred. When the symmetrical condition was in effect, every 10th correct left and every 10th correct right response was followed by food (10, 10). During the asymmetrical condition (1) every fifth correct left response was reinforced while every 25th correct right response was reinforced (5, 25) or (2) the probabilities were reversed so that every fifth correct right response was reinforced and every 25th left response was reinforced (25, 5). Nondrug baseline data were obtained for all subjects at all three consequence conditions, but drugs were administered at only two reinforcement frequencies for two birds (No 48 – 10, 10 and 5, 25; No. 37 – 10, 10 and 25, 5) and at one reinforcement frequency for the remaining two pigeons (No. 55 – 5, 25; No. 27 – 25, 5).

Pharmacological Procedure. Drugs were administered only after at least three consecutive days of stable responding, i.e., 5% or less daily variation in accuracy (percentage correct) for each stimulus duration. The following drugs and dosages were injected i.m. in random order in approximately 0.5-ml volumes no more than once a week to prevent any development of tolerance: 0.01, 0.04, 0.16 mg/kg of LSD; 1.0, 2.0, 4.0 mg/kg of AMP; 7.5, 15.0, 30.0 mg/kg of CPZ; 0.25 mg/kg of THC.¹ Except for THC, which was administered in the home cages 60 min prior to the session to insure maximum effect (Layman and Milton, 1971), all drugs were injected immediately before the sessions. All drugs were dissolved in isotonic saline except the THC, which was suspended in a Triton-X-100 solution diluted with saline. The Triton-X-100 occasionally served as the control injection on 'saline' days throughout the experiment and, like THC, was given 60 min before the animal was run. Saline or saline-diluted Triton-X control injection were administered after two successive days of stable responding.

¹ All doses refer to the salts. LSD was in the form of 0.1 mg/ml ampules of LSD-tartrate manufactured by Sandoz Pharmaceuticals and obtained from NIDA. Amphetamine (1 mg/ml) was prepared from *d*-amphetamine sulfate powder obtained from K and K laboratories, Plainview, New York. CPZ (7.5 mg/ml) was prepared from ampules containing chlorpromazine hydrochloride (Thorazine) obtained from Smith, Kline and French, Inc., Philadelphia, Pennsylvania. THC was prepared from 25-ml ampules of Δ^9 -THC dissolved in ethanol (1 mg/ml) obtained from NIDA. The ampules were subjected to vacuum to remove the alcohol, and the resinous THC was then suspended in 0.5 ml of Triton-X-100. The suspension was further diluted with 0.9% sodium chloride to a concentration of 1.0 mg/ml of THC.

Data Analysis. The effects of saline and of the four psychoactive drugs (LSD, AMP, CPZ, and THC) were analyzed on three measures of performance: (1) overall percentage correct, (2) percentage preference (i.e., responding on most frequently reinforced key or, in the case of 'symmetrical' schedules of reinforcement, percentage responding on the left key), and (3) reaction speed (i.e., the reciprocal of the time from onset of the house lights on each trial to the first center key response). The data on each of these measures under the two asymmetrical conditions (5, 25; 25, 5) were pooled ($N = 4$), and the mean absolute difference scores were compared a priori using Dunn's multiple comparison procedure (Kirk, 1968). For each compound, stability of baseline was evaluated by comparing mean absolute saline difference scores (saline day 2—saline day 3) prior to each dose; i.e., the difference score prior to dose 1 was compared to the difference scores prior to doses 2 and 3, and the difference score prior to dose 2 was compared to the difference score prior to dose 3; drug effects were evaluated by comparing mean absolute saline-drug difference scores (saline day 3—drug day) to their respective saline difference scores prior to each dose. Alpha (0.05) was divided equally among the six comparisons. No statistical comparisons were made on the data obtained under the symmetrical (10, 10) schedule because only two subjects were exposed to these conditions.

Results

The average accuracy (percentage correct) of the four birds run under both asymmetrical schedules of reinforcement (5, 25; 25, 5) during both control (mean of the three saline days preceding each dose of each drug) and drug sessions are shown, along with corresponding standard errors, in the top portion of Fig. 1. Even under control conditions, accuracy was rather low; that is, the mean percentage correct was never more than 70%. Statistical analysis (Dunn's procedure) indicated that baseline performance was stable; i.e., there were no significant differences in any of the comparisons of absolute saline difference scores.

Following all doses of every drug except 1.0 mg/kg of *d*-amphetamine, accuracy was lower than appropriate controls (Fig. 1, top) and, in general, these drug-induced decrements in performance were dose-dependent. They were statistically significant, however, only following THC (0.25 mg/kg) and CPZ (15 and 30 mg/kg).

The relative preference (percentage for the most frequently reinforced key in the four birds under asymmetrical schedules of reinforcement during both control and drug sessions is also shown in Fig. 1 (bottom portion). Even following saline injections, there is a considerable amount of variability in this measure both between subjects and within subjects over the course of the experiment; i.e., the average percentage preference varied between 64% and 78%, but the standard errors were often quite large (e.g., almost 13% during saline treatment prior to 30 mg/kg of chlorpromazine). There were, however, no significant differences in any of the comparisons of preference measures during saline sessions.

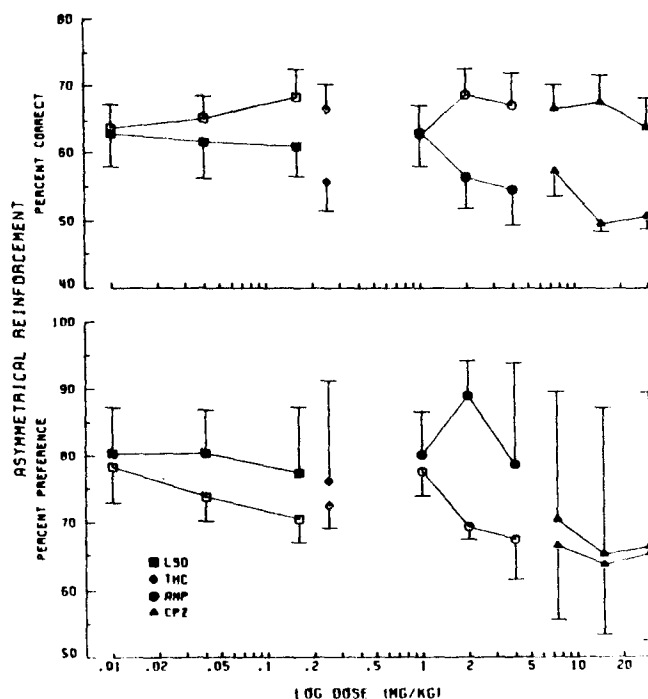


Fig. 1. Average accuracy (percentage correct) and preference (percentage responding on the most frequently reinforced key) of discrimination based on duration of visual stimuli in four birds exposed to asymmetrical schedules of reinforcement (5, 25 for birds B-48 and B-55; 25, 5 for birds B-27 and B-37). Open symbols: mean performance during 3 days of saline preceding each dose of each drug (dark symbols). Vertical bars: SEs

When drugs were administered, all of the birds changed their preference (criterion?) — particularly when doses were relatively high (Fig. 1, bottom). Following 0.16 mg/kg of LSD, 2.0 and 4.0 mg/kg of AMP, and 30 mg/kg of CPZ, these changes were statistically significant (when evaluated in terms of absolute differences between saline day 2 and day 3 vs. saline day 3 and drug). In some cases, the change was toward the more frequently reinforced key (i.e., an increase in preference); in other cases, however, the change was toward the less frequently reinforced key (e.g., following 30 mg/kg of CPZ). These effects are indicated in Fig. 1 (bottom) by the increase in standard error following drugs (even relative to the already large standard error following saline).

The accuracy (percentage correct) and 'preference' (left key) of the two birds (B-37 and B-48) exposed to the symmetrical (10, 10) schedule of reinforcement are shown in Fig. 2. In general, the accuracy of discrimination under these conditions (Fig. 2, top) is similar to those previously observed (Fig. 1, top). Following saline, percentage correct was low but reasonably stable (67–75%). All drugs except LSD appeared to reduce

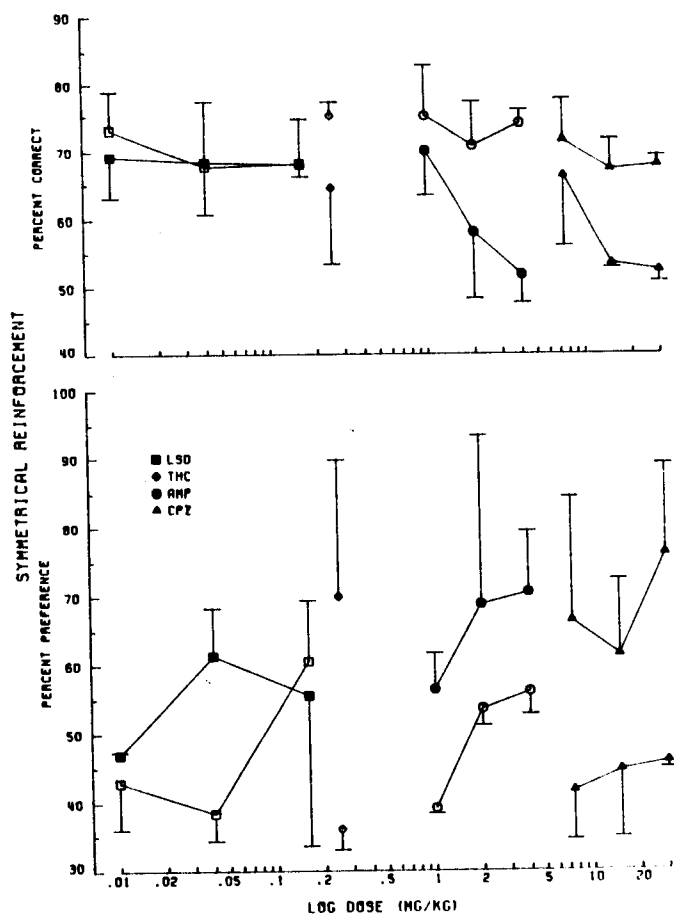


Fig. 2. Average accuracy (percentage correct) and preference (percentage responding on left key) of discrimination based on duration of visual stimuli in two birds (B-48 and B-37) exposed to a symmetrical (10, 10) schedule of reinforcement. Open symbols: mean performance during 3 days of saline preceding each dose of each drug (dark symbols). Vertical bars: SEs

accuracy — especially at relatively high doses; the data (from two animals) were not, however, subjected to statistical analyses.

The average speed (reciprocal reaction time) under both schedules of reinforcement are shown in Fig. 3. Under the asymmetrical schedule, speeds did not differ significantly when comparisons were made of saline difference scores.

LSD, which had no reliable effects on either of the discrimination measures (above), appeared to decrease response speeds at least as much as any other compound. When tested (under asymmetrical schedules), these decreases were significant at doses of 0.04 and 0.16 mg/kg. The single dose of THC (0.25 mg/kg) also decreased response speed significantly.

The effects of AMP and CPZ were more complex in that relatively low doses (e.g., 1.0 mg/kg of AMP and

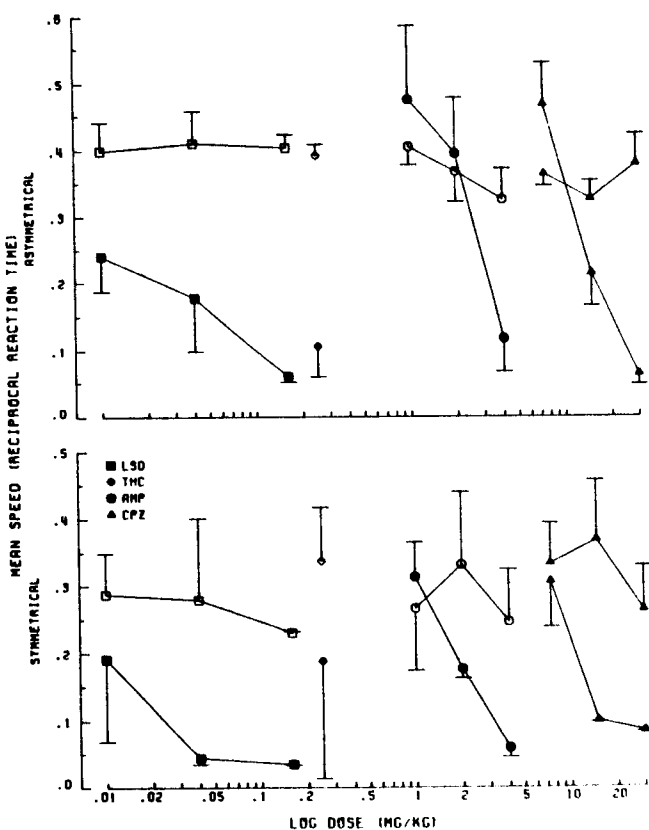


Fig. 3. Mean speed (reciprocal reaction time in seconds) of four birds (B-27, B-37, B-48, B-55) under asymmetrical (5, 25; 25, 5) and two birds (B-37, B-48) under symmetrical (10, 10) schedules of reinforcement. Open symbols: mean performance during 3 days of saline preceding each dose of each drug (dark symbols). Vertical bars: SEs

7.5 mg/kg of CPZ) appeared to increase speed under asymmetrical schedules, moderate doses had variable effects, and high doses decreased response speed, but only the disruptive effects of the highest doses (4.0 mg/kg of AMP and 30 mg/kg of CPZ) were statistically significant.

Discussion

The results, even though based on a small number of animals ($n=4$) and a restricted range of parameters (e.g., only two stimulus durations) are reasonably consistent with the literature involving similar experimental situations.

The data indicate that LSD (0.01–0.16 mg/kg) decreases response speed but otherwise has no signif-

icant effects on the accuracy of a discrimination based on duration. This result may seem surprising in view of the many reports of drug-induced distortions of time perception following ingestion of various hallucinogens in humans (above); it agrees, however, with most of the animal literature. For example, in unidimensional discrimination tasks, LSD has no effect on the detection of differences in visual intensity or brightness (Straub and Appel, 1975) in pigeons, or in either auditory frequency or duration (Dykstra and Appel, 1974) in rats (see also Appel, 1968). In squirrel monkeys, LSD has been reported to decrease the accuracy of a discrimination based on the duration of pure tones (Dykstra, 1972), but this effect has not been studied in many animals over a wide range of behavioral and pharmacological parameters. In any case, the extent to which reported differences in the effects of LSD are related to species-specific phenomena, procedural differences, or some other variable (e. g., task complexity) is not yet known.

The lack of change in accuracy following LSD cannot be attributed to an insufficiently high dose (0.16 mg/kg) for even lower doses effectively modify such other response measures as speed (in our experiment) and rate or response bias in other studies (Appel, 1968; Dykstra and Appel, 1974). Also, several extra test sessions were carried out at the end of the experiment using 0.64 mg/kg of LSD — a dose four times the previous maximum. There were no changes in accuracy even at this high dosage.

The results indicated that doses of 2.0 and 4.0 mg/kg of *d*-amphetamine lowered accuracy but did not do so significantly, perhaps because of the small number of subjects studied. Recent studies indicate more convincingly that this compound decreases the ability of both pigeons (Stubbs and Thomas, 1974) and rats (Rapp and Robbins, 1976) to discriminate durationally defined stimuli.

The increase in preference seen in the present experiment after *d*-amphetamine agrees with previous results (e.g., Stubbs and Thomas, 1974; Rapp and Robbins, 1976). It might be noted that humans given amphetamine show either an increase (Evans, 1969) or no change (Miller, 1960; Mackworth, 1965; Altman et al., 1975) in accuracy, and no shift in response perseveration. In human experiments, however, relatively low doses (10–15 mg), i.e., doses which have 'stimulant' properties (Goodman and Gilman, 1970), are invariably given (Miller, 1960; Evans, 1969; Altman et al., 1975).

Decreased accuracy in discrimination occurred in the present experiment following CPZ and THC. In animals, the phenothiazines can perhaps best be characterized in terms of their ability to attenuate both exteroceptive and interoceptive stimulus control

(Iversen and Iversen, 1975), and, in normal humans (i.e., patients not classified as paranoid-schizophrenic), phenothiazine-induced decreases in sensitivity to stimuli that differ on the bases of auditory intensity (loudness) have also been reported (Rappaport et al., 1971).

The decrease in accuracy produced by THC is also supported by at least three studies. Abel (1971) and Zeidenberg et al. (1973) tested humans given marijuana cigarettes or THC capsules, respectively, and demonstrated a significant decrease in their ability to recognize words after a specified delay. Abel (1971) also found an increase in response perseveration. In an experiment investigating the detection of auditory signals, Moskowitz and McGlothlin (1974) reported a dose-related decrement in sensitivity following marijuana administration to 23 males.

Although not subjected to statistical analysis, the results of the present experiment suggest that, regardless of which compound is administered, the effects of drugs on accuracy are often accompanied by substantial increases in perseveration. Changes in percentage correct are not, however, always accompanied by such changes (especially at lower doses), and perseveration does not always occur on the most frequently reinforced key (in the case of asymmetrical schedules of reinforcement).

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All figures were plotted by Calcomp Plotter (Computer Services Division, University of South Carolina) with the assistance of Ms. Agnes Rahon. An interactive software package (API) developed by William T. McGowan was used to generate Fortran commands necessary to drive the plotter.

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