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Some Effects of Lysergic Acid Diethylamide on Visual Discrimination in Pigeons*

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Lysergic acid diethylamide (LSD) has a number of reasonably well established general effects upon operant behavior. Transient interruption of responding ("pausing") has been observed in rats (Appel and Freedman, 1964; Freedman *et al.*, 1964; Liberson, Ellen, Schwartz, Wilson, and Gagnon, 1962; Olds and Olds, 1964; Ray, 1965), guinea pigs (Liberson *et al.*, 1962), pigeons (Berryman, Jarvik, and Nevin, 1962), and rabbits (McGaugh, de Baran, and Longo, 1963). The tasks involved included responding for food on simple schedules of reinforcement, hypothalamic self-stimulation, approach behavior and complex discrimination learning (matching to sample). Similarly, depression or lowering of response rate has been seen in monkeys (Jarvik and Chorover, 1960), rats (Jarrard, 1963; Freedman *et al.*, 1964; Ray, 1965), humans (Ostfeld, 1961) and pigeons (Blough, 1957a). As would be expected, increase in reaction time is another common finding with LSD (Berryman *et al.*, 1962; Edwards and Cohen, 1961; Fuster, 1957, 1959). Tolerance to the behavioral effects of LSD has also been investigated (Freedman *et al.*, 1964).

Several experiments have been concerned with an interesting and perhaps clinically relevant problem of how LSD specifically affects visual and auditory perception. In man, LSD increases the brightness threshold (Carlson, 1958) and alters the shape of the dark adaptation curve (Ostfeld, 1961). Similar threshold data were reported for the pigeon (Blough, 1957b). In cats, Key (1961, 1964) found that low doses of LSD (*i. e.* 10—15 μg/kg) increased generalization of both auditory and visual stimuli.

The effects of LSD upon accuracy of perception are less clear because of differences in dose level, species, and nature of the tasks studied. The drug impaired monkeys' performance of a delayed alternation task

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(JARVIK and CHOROVER, 1960) and visual discriminations (FUSTER, 1957, 1959), but no change in accuracy was noted in auditory discrimination in cats (KEY, 1961) or in matching behavior in the pigeon (BERRYMAN, *et al.*, 1962). BLOUGH (1957a) found an increase in accuracy of a complex brightness discrimination in pigeons, an effect which outlasted the depression of response rate which followed drug administration.

The present experiments are, as those of BLOUGH, concerned with the effects of LSD on a visual discrimination in the pigeon. In an attempt to clarify the relationship of LSD to both accuracy and rate, dose and difficulty of perception were experimentally varied in a latin-square design. The procedure also permitted study of the effect of the drug on food consumption (HAMILTON and WILPIZESKI, 1961) and the development of long-term tolerance to LSD.

The task was designed so that the difficulty involved was primarily "perceptual". The pigeons were well trained prior to drug administration and a minimum of "problem-solving" was needed for the bird to make the correct response. The discrimination was between flickering and steady light; the task difficulty could be altered by increasing the frequency of the flickering light.

It is apparent that, as the flicker frequency is increased, a point will be reached at which the flickering light appears steady. This is the critical flicker frequency (CFF), a phenomenon which has been extensively investigated. It should be noted that, in the present study, CFF values were not specifically relevant; CFF of the flickering light only means that the discrimination between flicker and steady has become impossible. Nevertheless, it is of interest that depressants of the CFF include barbiturates (AIBA, 1959), phenothiazines (HOEHN-SARIC, BACON, and GROSS, 1964; KARP and POLLACK, 1963; LLOYD and NEWBROUGH, 1964), nitrous oxide (HOLLAND and GOOCH, 1962), carbon monoxide (VON POST-LINGEN, 1964), electroconvulsive therapy (MOWBRAY, 1961) and brain damage (TARAVELLA and CLARK, 1963). Depression of the critical flicker frequency means, in these studies, that subjects discriminate between flicker and steady less well, while elevation of the CFF implies a better discrimination. Although the results of two recent experiments are contradictory (HOLLIDAY, HALL, and SHARPLEY, 1965; LANDIS and CLAUSEN, 1954) there is reason to believe that LSD should elevate the CFF. Two drugs related in some ways to LSD-*d*-amphetamine (AIBA, 1959) and psilocybin (KEELER, 1963)—both elevate this perceptual measure in man. Psilocybin is both chemically and clinically analogous to LSD, producing much of the same hallucinatory experiences and classed as a "psychotomimetic". Amphetamine yields some behavioral changes similar to those of LSD (HAMILTON, 1960) and clinically, large, prolonged doses of amphetamine may also be "psychotomimetic".

Method and Materials

Subjects. Six male White Carneaux pigeons, 3 months old, obtained from Palmetto Pigeon Plant, Sumter, S.C., were permitted to eat *ad. lib.* for 5 days in individual home cages, and a free-feeding weight was obtained for each bird. The pigeons were then reduced to 80% of this weight by feeding 5 g daily of a mixture of 40% vetch, 50% Kaffir corn and 10% hemp seed. This was the food mixture used throughout the entire period of study. Birds were maintained at 80% free-feeding weight by supplementary feeding in their home cages immediately following an experimental session. Water was always available in home cages which were housed in a room of constant temperature and humidity with a 12 hr light-dark cycle.

Apparatus. The experimental box was a modified version of that described by FERSTER and SKINNER (1957). Two keys which could be transilluminated were placed two inches apart and equidistant from the food magazine. When the magazine was opened to make food available to the birds for 3 sec, a loud click occurred and the food was illuminated by a small light bulb placed high in the magazine structure. White noise was generated in the box to remove the distraction of external sound in the lab. The small house lights were gradually dimmed and finally extinguished before actual testing was begun, so that the only illumination in the box was provided by lights behind the translucent keys.

Two lights behind each key (General Electric Neon NE 51) were connected in parallel to the output of a tachistoscopic timer (R. C. Gunter Associates, Charlton, Mass.) which was driven by a square-wave stimulator (Bio-Electronic Laboratory, Div. of TALCO Engineering Co., Inc., Hamden, Conn.). The purpose of the above apparatus was to provide a controlled source of flickering light. The intensity and duration of the *on* phase were regulated by controls on the tachistoscopic timer. The frequency of the flicker, that is, the number of *on* pulses per second, was controlled by the square-wave stimulator.

The intensity of the lights was maintained at a constant level throughout all experiments. In addition, for practical reasons, the duration of the *on* phase, *i.e.*, the pulse width, was kept at 4 msec. The flicker frequency was varied (below). It is apparent then, that as the frequency of flicker was increased, the total *on* time of the lights was increased also. For example, at a flicker of 30 cycles per second, the lights are on for 30×4 msec or 120 msec per second. At a flicker of 50 cps the *on* time is 200 msec/sec. Thus a discrimination between two flicker frequencies may involve the number of *on* pulses per second, the duration of the *on* phase or both. The advantage of using this type of task is that its difficulty can be easily and continuously varied by adjusting the flicker frequencies of the stimuli which are to be discriminated.

In practice, the pigeons were required to discriminate between a flickering and a "steady" light. A flicker of 100 cps was used for the "steady" condition. The lights behind both keys were operated together. When the lights were "steady," only pecks on the left key in the box were rewarded. At randomized, pre-set intervals, the condition was switched to "flicker." The lights then flickered at the desired frequency for the specific day's run, and only pecks on the right key were rewarded. The average length of each flicker or steady interval was 40 sec.

The various conditions were programmed automatically by relay and timing circuits located in an adjoining room. Counters recorded responses on each key for both flickering and steady intervals. Two cumulative recorders were also used, one for correct responses (left key pecks on "steady," right key pecks on "flicker") and one recorder for errors.

Behavioral Procedure. Three experiments were run during a 10 month period. Throughout all experiments the number of correct responses necessary to obtain a reinforcement was 35 (FR 35); incorrect responses were never rewarded. All experimental sessions were terminated automatically as soon as 60 reinforcements were given. For the first experiment, the discriminations 30 cps *vs* steady, 50 cps *vs* steady and 70 cps *vs* steady were run. Experiment II was identical in all details except that flicker levels of 50, 55, 58, 62, 66 and 71 cps were employed; Experiment III investigated discriminations of 10, 20, and 30 cps *vs* steady.

Pharmacological Procedure. LSD in ampules of 0.1 mg/ml was obtained from Sandoz Pharmaceuticals, Hanover, N. J. The drug was administered in doses of 20 μg per kilogram, 40 μg/kg and 80 μg/kg to each bird at each flicker level. Each LSD day was preceded by a physiological saline control day run at the same flicker frequency, and followed by a non-injection control day. Thus in the first experiment there were nine different 3-day runs for each of the six pigeons, one at each dose level for each flicker level. All saline and LSD doses were administered by intra-muscular (i.m.) injections approximately 1 cm lateral to the sternum, immediately before the start of the experimental session.

Results

The effects of LSD upon accuracy of the visual discrimination will be considered first; other dose-response data will follow.

Experiment I

A major purpose of this experiment was to explore the range of flicker frequencies the pigeon can discriminate from "steady" under the experimental conditions. To accomplish this, flicker frequencies of 30, 50 and 70 cycles per second were used.

Performance under LSD was always compared to the birds' performance on the identical task run the day before under NaCl. Although

three dose levels of LSD appear to increase the accuracy of the discrimination 30 cps *vs* steady light (Fig. 1), this increase is not statistically significant (t-test for differences, $p < .20$). Because the birds do very much worse on the 70 cps *vs* steady discrimination than they do on either the 30 or the 50 cps *vs* steady discrimination (Fig. 1), the data suggest that the range between 50 and 70 cycles per second flicker might be worth exploring.

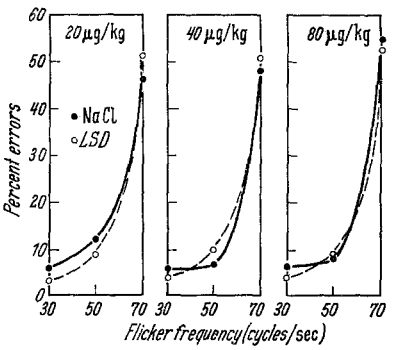

Fig. 1. Experiment I: Per cent errors by LSD dose and flicker frequency, average of six birds

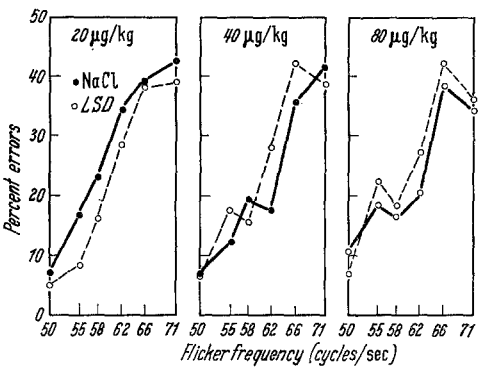

Fig. 2. Experiment II: Per cent errors, saline and three LSD doses, shown for each flicker frequency, average of six birds

Experiment II

Six closely spaced levels of flicker frequency were used: 50, 55, 58, 62, 66, and 71 cps; drug doses, as before, were 20, 40, and 80 µg LSD/kg. In order to determine the degree of covariance of increasing drug dose and increasing task difficulty (increased flicker frequency) with respect to errors, a non-parametric equivalent of an analysis of variance was performed (WILCOXON, 1949); the degree of interaction was not significant ($p < .12$).

Number of errors is an increasing, monotonic, function of flicker frequency (Fig. 2). The correlation of these variables is significant by the WILCOXON (1949) rank test ($p < .001$).

Fig. 2 shows average errors combined for all birds, at each flicker frequency and each drug dose. It is evident that at each flicker level, 20 μg LSD/kg reduced the birds' average errors. The *t*-test for differences is significant here at $p < .02$. Eighty μg/kg raised errors at five out of six flicker levels but this effect was not significant ($p < .12$).

Experiment III

The increased accuracy of the birds on the 30 cycles per second discrimination found at all drug doses in Experiment I prompted a further investigation of the area of the "easy" discrimination. For this experiment, flicker levels of 10, 20, and 30 cps were used. No major effect of LSD on errors was found, although at both 20 and 30 cps, 20 μg/kg improved performance. The lack of a clear effect can perhaps be ascribed to the fact that the task was too easy, i.e., there was not much room for improvement.

Table. *Per cent errors, NaCl vs 20 μg LSD/kg, averaged over 6 birds*

	Flicker frequency (cps)	NaCl	20 μg LSD/kg
EXP. I	30	5.9	3.2
	50	11.9	8.5
	70	46.1	50.8
EXP. II	50	7.1	5.1
	55	16.9	8.6
	58	23.1	16.2
	62	34.6	28.9
	66	39.1	39.0
	71	43.7	39.2
EXP. III	10	7.3	8.0
	20	3.1	3.0
	30	8.3	4.4

The Experiments Combined

The most interesting result of the three experiments with regard to errors was the effect of 20 μg LSD/kg. These data are shown in the table. At nine of the eleven flicker level runs in the experiments, LSD at this dose improved accuracy on the visual discrimination. The *t*-test for differences is significant ($p < .05$).

Dose-response data

The dose-response results were similar for all three experiments and will be considered together.

Drugs can and usually do affect average or overall rate as well as accuracy of performance. On a ratio schedule such as that used in these experiments, LSD generally depresses the overall rate by introducing one or more periods of no-responding or "pausing" the duration of which depends upon dose (FREEDMAN *et al.*, 1964). But overall rate could also be affected by slower key-pecking. For these reasons, three "rate"

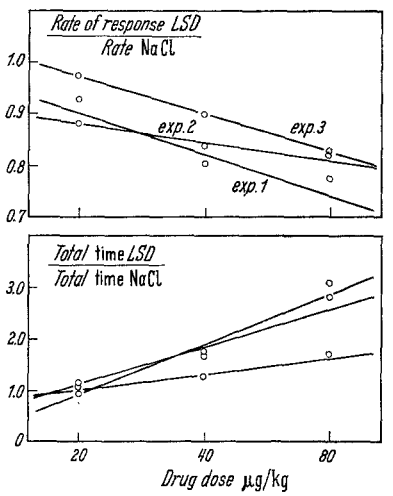

Fig. 3

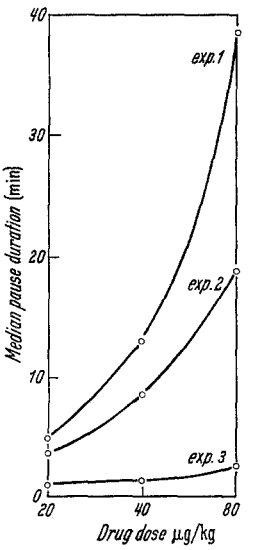

Fig. 4

Fig. 3. Dose-response measures: $\frac{\text{rate of response/LSD}}{\text{rate of response/NaCl}}$ and $\frac{\text{total time/LSD}}{\text{total time/NaCl}}$ by LSD dose for each experiment, average of six birds

Fig. 4. Median pause duration by LSD dose, shown for each experiment, average of six birds

measures are plotted as functions of dose; (1) *total time* to receive 60 reinforcements, which reflects amount of pausing, changes in running rates, or both, (2) *running rate*, which is the rate during times when the animal is not pausing for any perceptible length of time as indicated by its cumulative record, and (3) median pause duration.

In Fig. 3, *total time* per drug session is divided by total time in the NaCl session the day before. At all dose levels, as shown, the quotient is greater than one since total time under LSD is greater than total time for saline. *Running rate* per drug session was divided by running rate for the NaCl session of the previous day. At all dose levels, this quotient was less than one. These results are dose-related and hold up through all three experiments, although the effect seems to be less in the third experiment than in the previous two.

Occasionally at the 20 μg/kg dose level, and more often at the higher levels, the bird would stop responding altogether. This is the typical response to LSD ("pausing") shown by animals on FR schedules (FREEDMAN *et al.*, 1964). Frequency of pausing increased with drug dose in all three experiments; thus LSD both increases the amount of pausing and decreases actual *running rate* in a dose-related manner.

The median pause duration data are shown in Fig. 4. It will be noted that pause duration increases with drug dose in each experiment. In addition, the data show that at each dose, pause duration decreases from one experiment to the next despite the fact that the number of pauses did not decrease. This suggests that some sort of long-term tolerance to this effect of the drug has developed. An interval of approximately 6 weeks elapsed between Experiments I and II and an interval of 3 weeks between Experiments II and III during which time the animals were not given LSD. This should have been sufficient for the pigeons to break tolerance and return to starting levels of pause duration.

Food Consumption

There have been suggestions both clinically and experimentally that LSD decreases food consumption (above). An attempt to verify these impressions was made.

Each bird was weighed immediately before and directly after each experimental session. Since 60 three-second reinforcement periods occurred during each session, comparisons between sessions regarding food consumption were possible. The data from Experiment II were examined since, by the time that experiment was run, defecation by the birds during the discrimination test (presumably due to the novelty of the experimental environment) had ceased to occur. Average weight gain per session after LSD was always less than after saline, e.g. 5.3 g for 80 μg LSD/kg and 7.7 g for saline but these differences were not significant ($p < .07$ and $p < .08$ respectively).

Discussion

The reason for the significant increase in accuracy following 20 μg LSD/kg is not readily apparent, although some previous research suggested an enhancement of visually-controlled performance by LSD (BLOUGH, 1957a; LANDIS and CLAUSEN, 1954).

If decreased rate of response accounted for the improvement, then the decline in accuracy with increasing dose would be difficult to explain. The idea that perhaps it is apparent brightness discrimination which is enhanced is in conflict with increases in brightness generalization found with LSD (KEY, 1964).

Some neurophysiological evidence (SCHWARTZ and CHENEY, 1965a, 1965b) indicates that LSD treatment yields electrical responses not

unlike those found when the retina is stimulated with flickering light. Perhaps the increase in accuracy is specific to the nature of the discrimination, that is, LSD makes lights look as if they are flickering. If this effect were most powerful when the lights were actually flickering just above the CFF, then LSD would have the effect of raising the "threshold". But the fact that LSD increased accuracy over the entire range of flicker frequencies tested, even when the birds were doing as well as 94% correct, dispels the notion of a simple increase in "threshold" as the explanation for the results.

BLOUGH (1957a) tested pigeons on a task which required responding on one or the other of two keys, depending upon whether a light in the box was on or off. The accuracy of performance under these conditions was improved by LSD. It is unlikely that the drug made it easier for the pigeon to tell whether the light was on or not. What is possible is that the drug somehow increased the "importance" of the light; that is, responses to distracting stimuli were less likely to be emitted under the drug. Thus in the present series of experiments, LSD may have given flicker a "sensory impact" which it did not possess or possessed to a lesser degree under saline, making it impossible for the change from steady to flicker to go unnoticed.

With relatively low doses of drug, *e.g.*, 20 μg/kg, this increase in "stimulus visibility" has the effect of improving accuracy of performance on visual discrimination tasks which are well-learned. At high doses, LSD may intensify all stimuli to such a degree that perceptual disorientation is the result, and accuracy declines.

Depression of response rate might be a result of general motor incoordination due to LSD; however, behavioral data on wheel-turning (APPEL *et al.*, 1967) and running responses (HAMILTON, 1960) do not support this hypothesis. Descreased response rate may more probably be due to a descreased "interest" of the animal in the task, and possibly to an LSD-induced decrease in the reinforcing value of food (HAMILTON and WILPIZESKI, 1961).

Long-term tolerance to the effects of LSD is reflected by the progressive decline in pause duration from one experiment to the next. The fact that the median starting time of the pauses did not change may imply that this phenomenon is related to physiological and pharmacological factors such as length of time necessary for the drug to reach its "active site" in the brain; in any case, previous data confirm that tolerance is not learning (FREEDMAN *et al.*, 1964).

Summary

Six pigeons were tested on a visual discrimination between light flickering at various frequencies and a steady light, under saline and

LSD. The birds were required to respond for food rewardby pecking on the left key in the experimental box at FR35 if the light was steady, and at FR35 on the right key if the light flickered. Incorrect responses were never rewarded. Each experimental session continued until the bird obtained 60 reinforcements.

The doses of LSD were 20, 40, and 80 μg/kg, administered by i.m. injection. 20 μg/kg produced a significant increase in accuracy of performance and the results with 80 μg/kg suggest a decrement in accuracy. Depression of the rate of responding as well as periods of complete cessation of responding were found to occur in dose-related fashion. Tolerance to the rate and pause effects apparently developed over the testing period of about 10 months.

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