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QUANTIFICATION OF THE EFFECTS OF CHLORPROMAZINE ON PERFORMANCE UNDER DELAYED MATCHING TO SAMPLE IN PIGEONS

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The effects of four doses of chlorpromazine (dose range 0.5 to 12.5 mg/kg) on performance under a delayed matching-to-sample procedure in pigeons was investigated, using the exponential model of memory (White, 1985). Performance was measured using a bias-free measure of discriminability, log d (Davison & Tustin, 1978), and negative exponential functions were fitted to individual-subject and group data at each dose level. A decrease in matching accuracy was found to be caused by an increase in the rate of forgetting, b, and a decrease in the initial discriminability, log d_0. Changes in rate of forgetting and discriminability occurred at doses that had no statistically significant effect on response latency. The exponential model of memory accounted well for the data and provided a useful way of quantifying the effects of chlorpromazine on the processes involved in delayed matching-to-sample performance.

Key words: delayed matching to sample, memory, forgetting, chlorpromazine, key peck, pigeons

In the experimental analysis of behavior, memory, or remembering, is viewed as the control of a discriminated operant in the absence of the discriminative stimuli (Catania, 1979). Memory can, therefore, be studied using the same procedures as those used to study discrimination, with the exception that a delay occurs between the presentation of the stimulus "to be remembered" and the occasion for the response (White, 1985). Different behavioral processes are assumed to be involved depending on the duration of the delay (Heise & Milar, 1984). For example, in the widely used matching-to-sample (MTS) procedure, subjects are reinforced for choosing the comparison stimulus that matches the sample stimulus. When there is no delay and the choice response is made in the presence of the sample stimulus, it is assumed that only discrimination processes are involved. When there is a delay between the sample and comparison stimuli, and the response is made in the absence of the sample stimulus, as in a delayed matching-to-sample (DMTS) procedure, both discrimination and memory processes are assumed to be involved.

The DMTS procedure has been used to evaluate the effects of various drugs on short-term memory (Thompson, 1978). One such drug is the widely used neuroleptic, chlorpromazine (CPZ). Clinical studies in humans have suggested that at higher doses, CPZ may impair learning and memory processes (Aman, 1984; Aman & Singh, 1983; Werry, 1988). Because CPZ is used in the developmentally delayed population, any such drug-induced side effects on learning and memory are of concern. This clinical concern makes an evaluation of the effects of CPZ on delayed discrimination procedures like DMTS relevant.

Three studies have examined the effect of CPZ on delayed discrimination procedures in primates. In one study, monkeys were trained on a delayed color matching task in which the delay intervals varied from 0 to 32 s. It was found that CPZ (dose range 0.05 to 0.40 mg/kg) decreased response rate, but that the percentage drop in accuracy was small unless accompanied by a large decrease in response rate (Glick, Goldfarb, Robustelli, Geller, & Jarvik, 1969). This finding was replicated by Robustelli, Geller, and Jarvik (1968), who concluded that CPZ had no specific effect on short-term memory because the depressant effect occurred irrespective of the delay interval.

In a further study, Roberts and Bradley

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(1967) trained African green monkeys on a same–different color discrimination task. At the beginning of a trial one half of a response panel was illuminated with either red or green light. After a delay of 0, 3, 5, or 7 s, the other half of the panel was illuminated with either red or green light. The monkeys' task was to press the panel if the colors were different but to refrain from doing so if the same colors were presented. A dose of 2.5 mg/kg of CPZ resulted in a statistically nonsignificant 4.3% average decrease in mean matching accuracy over all delays, whereas a 5.0-mg/kg dose resulted in a statistically significant 13.6% decrease in mean matching accuracy. Although the mean accuracy score at each delay suggested that the decrement in matching accuracy became greater at the longer delays, there was no statistically significant relationship between delay interval and mean matching accuracy. In addition, because of the similarity in the effects of CPZ and the sedative-hypnotic drug pentobarbitone, the authors concluded that the effects of the higher dose of CPZ were due primarily to its sedative action rather than to any specific effect on short-term memory.

There are two problems with these and many other studies evaluating drug effects on memory. The first concerns the use of the percentage correct measure to assess performance. This measure is known to be influenced by two factors: perceptual sensitivity (or discriminability) and response bias. Signal-detection theory (Green & Swets, 1966) has been successful in separating these effects, which are otherwise confounded when the percentage correct measure is used (Wright, 1974). Although some researchers have used formal indices of sensitivity and bias in the evaluation of the effects of CPZ (e.g., Appel & Dykstra, 1977), other studies have recognized the importance of differentiating perceptual sensitivity and response bias but have not carried out a formal detection analysis (Altman, Appel, & McGowan, 1979; Hernandez & Appel, 1979). This, coupled with the use of different procedures, doses of CPZ, and species, makes an interpretation of the effects of CPZ on perceptual sensitivity and response bias difficult. In addition, in the case of CPZ, detection analyses have been applied only to no-delay or zero-delay discrimination procedures.

Even if measures of perceptual sensitivity and bias were used to assess performance in delayed-discrimination procedures, their use would not overcome the second problem that exists in analyzing the results of drug studies, that is, determining whether discrimination or memory processes are being affected. Usually a comparison is made of the accuracy of performance by delay interval curves for a control and drug condition. Drug effects on memory or retention are assumed to be represented by differences in the slopes of these curves. Drug effects that result in displacement of the control curves, with no change in slope, are assumed to involve discrimination processes. However, there is little standardization in this analysis, and problems exist in which floor and ceiling effects can produce divergence and convergence in the control and drug curves (Heise & Milar, 1984).

Recently, quantification of remembering in terms of a negative exponential function has been proposed (McCarthy & White, 1987; White & McKenzie, 1982), and the application of this analysis to drug effects has the potential to overcome the two problems outlined above. This analysis proposes that the forgetting function relating performance under delayed stimulus control to the length of the delay has two characteristics (White, 1985). The first characteristic is the initial level of stimulus control (i.e., the strength of the stimulus control when there is no delay between the stimulus to be remembered and the presentation of the stimuli to which a response is made). The second characteristic of the forgetting function is the rate at which this initial stimulus control declines as the delay interval increases.

In the negative exponential analysis, performance at the different delay intervals is quantified using a measure of discriminability, log d, derived from the application of the generalized matching law (Baum, 1974) to the standard signal-detection payoff matrix (Davison & Tustin, 1978). In yes–no detection or two-choice discrimination procedures, the subject is trained to make one response, P1, when one stimulus, S1, is present and another response, P2, when the other stimulus, S2, is present. The resulting stimulus and response matrix is shown in Figure 1, in which W, X, Y, and Z refer to the cells of the matrix. If P denotes responses, Pw is the number of responses in Cell W and Px is the number of responses in Cell X. Davison and Tustin (1978)

argued that the choice between P1 and P2 in S1 or S2 was determined by the overall rate of reinforcers for correct P1 and P2 responses, according to the generalized matching law.

The effect of the stimuli is to bias the choice in S1 towards P1 and the choice in S2 toward P2. Because the effects of this stimulus bias are equal and opposite in the two stimuli, the equations describing the concurrent choice in each stimulus are modified by a constant that describes the discriminability, d, between the stimuli. When equations for the concurrent choice in the two stimuli are combined, the terms describing the biasing effects of reinforcers and sources of constant bias cancel out. The result is a bias-free measure of stimulus discriminability:

$$\log d = 0.5 \log(\mathrm{PwPz}/\mathrm{PxPy}). \quad (1)$$

Discriminability, log d, at the different delay intervals has been used to quantify performance in which a delay, t, is interpolated between the sample and comparison stimuli in a detection or a discrimination task. The exponential model for remembering developed from the finding that log d decreased as a negatively accelerated function of increasing delay interval for both single-stimulus and relation-recall procedures (White & McKenzie,1982). It was assumed that discriminability decremented as a negative exponential function of time according to the following equation:

$$\log d_t = \log d_0 \cdot e^{-bt} \quad (2)$$

where log d_0 is the discriminability at time t = 0, and b is rate of forgetting (with units of $1/t$). White (1985)[1] has referred to the exponential model in Equation 2 as a model of "direct" remembering because the rate at which discriminability declines in the function is constant. That is, the exponential decrease in discriminability allows remembering to be treated in the same terms as discrimination, except that remembering involves the discrimination of temporally distant stimuli. Remembering is thus direct (as in Gibson's, 1979, theory of "direct perception"), rather than indirect as in traditional theories of memory in which information processing mediates between stimulus presentation and behavior.

Equation 2 has been found to account well for the data obtained in delayed discrimination experiments using both animals and humans

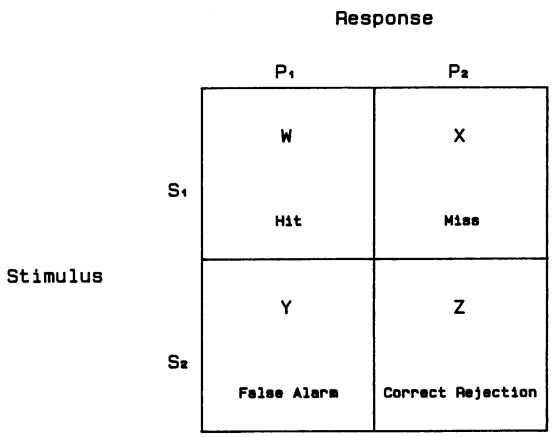

Fig. 1. The matrix of stimulus and response events in a two-choice discrimination procedure. The letters W, X, Y, and Z denote the number of events in each cell.

(McCarthy & White, 1987). Further it has been proposed that the parameters describing the decay functions, log d_0 and b, are independent (White, 1985).[1] This proposal is supported by the finding that log d_0 is affected by characteristics of the sample stimulus, with no accompanying change in b (White, 1985; White & McKenzie, 1982)[1] and that b changes independently of log d_0 when rehearsal or retrieval processes are disrupted by houselight illumination during the delay interval (White, 1985). These findings support the notion that initial discriminability, log d_0, provides a measure of discrimination processes, whereas b is a measure of memory or retention processes.

The exponential model of memory appears to provide an explicit means of quantifying drug effects on discrimination and memory processes. The model has been successfully used to describe the effects of the anticholinergic drug scopolamine on the performance of an auditory delayed matching-to-sample task in rats. Kirk, White, and McNaughton (1988) reported that scopolamine (dose range 0.005 to 0.375 mg/kg) caused a highly significant decrease in initial discriminability, log d_0, whereas the rate of forgetting, b, only showed a slight increase at the highest dose level. The

[1] Also: White, K. G. (1987). *Psychophysics of direct remembering.* Paper presented at the tenth Harvard Symposium on Quantitative Analysis of Behavior: Signal Detection. Cambridge, Massachusetts.

results were seen as providing theoretical and pharmacological support for the notion that initial discriminability and rate of memory decay are independent parameters.

The aim of this study was to use the exponential model of remembering to quantify the effects of CPZ on the performance of pigeons in a delayed matching-to-sample task. A second aim was to evaluate further the independence of the initial discriminability, log d_0, and the rate of forgetting, b.

METHOD

Subjects

Subjects were 5 experimentally naive homing pigeons obtained from local suppliers. They were maintained at 80% of their free-feeding body weights by supplementary feeding in their home cages after each session. They were housed individually with unlimited access to water and grit in a room heated to 24 ± 3 °C and illuminated from 6 a.m. to 6:30 p.m.

Apparatus

Four standard experimental chambers, 50 cm deep, 50 cm high, and 20 cm wide, were used. In each chamber, three response keys, 2.3 cm in diameter, were located 23 cm from the bottom of the intelligence panel (front wall) and 8 cm apart. The middle key was centered on the front wall. Each key could be illuminated with red or green light. A minimum force of 0.2 N was required for key operation. A centrally located aperture 6 cm from the floor gave access to a hopper filled with grain. Each chamber was ventilated by a fan that also provided masking noise. There was no houselight. A PDP® 11/10 computer controlled experimental events and collected the data.

Procedure

Throughout the training and subsequent experimental phases of the study, sessions were conducted at approximately the same time each day, 7 days per week. Each bird was initially trained to eat grain from the raised and lighted food hopper and was then trained to peck the center key when it was illuminated using the autoshaping procedure (Brown & Jenkins, 1968). Pecks to the illuminated center key resulted in 3-s access to the hopper.

Initial training. Each daily session consisted of 72 trials. A trial began with the illumination of the center key with either a red or green sample stimulus. A fixed ratio (FR) of five pecks was required to extinguish the sample. The center key latency was defined as the time to complete the FR 5. When the center-key ratio was complete, the stimulus on the center key was immediately darkened and the side keys illuminated, one each with red and green. A response to the stimulus matching the sample produced food. Responses to the nonmatching key resulted in a 3-s blackout. The side-key latency was the duration of the comparison stimuli. Between each trial there was an intertrial interval (ITI) of 25 s. When the subjects were reliably performing at 90% to 95% correct on this procedure (after approximately 25 sessions), the DMTS procedure was introduced.

Delayed matching-to-sample training. Delays were introduced between the presentation of the sample and the comparison stimuli. The delays used were 0, 1, 2, 4, 8, and 16 s arranged in a random order within a session. The number of trials per session was 120 (10 of each color sample per delay), and the ITI was 15 s. The distribution of the sample stimulus colors (red and green) on the center key was random with the exception that no more than three consecutive sample stimuli were the same color. The distribution of the comparison stimuli on the side keys (i.e., red-left and green-right or green-left and red-right) was random except that on no more than three consecutive trials was the same color in the same position. In addition, the matching color could occur on one side on no more than three consecutive trials. Reinforcers for correct responses were arranged to equate the probability of reinforcing correct left and right responses to red and green stimuli. In addition, 50% of correct responses over all trials within each session were reinforced. That is, reinforcers obtained for correct responses to red and green stimuli (and on left and right keys) were approximately equal and approximated half the number of correct responses emitted at each delay interval. Nonreinforced correct trials resulted in a 3-s blackout.

Training on the DMTS procedure continued for 6 months until all the subjects met the two stability criteria used by Harnett, McCarthy, and Davison (1984). The first was that the median proportion of correct responses over five sessions be within .05 of the median proportion correct from the preceding five ses-

sions. This criterion had to be met five, not necessarily consecutive, times by each bird. The second criterion was that there be no increasing or decreasing trends in the discriminability (log d; Equation 1) for each bird over consecutive training sessions.

Drug administration. Four doses of CPZ were tested: 0.5, 2.5, 5.0, and 12.5 mg/kg. The drug was obtained from commercial suppliers in 25 mg/mL, 1-mL ampules and was diluted to the required concentration with isotonic saline. Each bird was given three administrations of each dose in a random order. Vehicle control injections (isotonic saline) were given on the day immediately preceding each drug injection. All injections were given in a volume of 1 mL/kg intraperitoneally 15 min before the start of the session. Between any one injection of CPZ and the next saline injection there were at least 2 days. The proportion of correct responses had to be within .05 of the mean proportion correct during baseline before the next injection was administered.

RESULTS

For each bird, correct and incorrect responses were summed across the three administrations of each drug dose (individual analysis); data were then summed across birds (group analysis).

The Effect of Vehicle Control Injections

Using grouped data, an analysis of the effects of vehicle control injections on the variables assessing matching responses (percentage correct) and psychomotor performance (center- and side-key latencies) was carried out. This showed that performance in the vehicle control condition was not significantly different from baseline performance. Therefore 3 days on which vehicle control injections were given were chosen at random, and the data were summed to form the composite vehicle control condition. This was used as the control condition in subsequent analyses of the drug effects.

The Effect of CPZ on Matching-to-Sample Performance Percentage Correct

The number of correct choices at each delay for each drug condition and each bird is presented in Appendix A. From these data the percentage correct for each bird for each delay interval across the drug doses was calculated. These data are presented in Figure 2.

Performance in the vehicle control condition was high for all birds, especially at the 0-, 1-, and 2-s delay values. As the delay value increased the percentage correct decreased, but performance for all but Bird 5 remained 70% correct or higher at the 16-s delay. Increasing doses of CPZ decreased percentage correct, usually across all delay values, although for most birds performance at the 0-s delay remained close to the control condition level. The drug did not appear to change the performance of Bird 5 from control levels.

Percentage correct was also calculated for the group data for each delay interval as a function of drug dose. These data are presented in Figure 3. The pattern shown in Figure 3 supports the conclusion reached for the individual analysis, that is, a decrease in percentage correct with both increasing delay value and increasing drug dose. As the dose increased, performance at the 0-s and 1-s delays remained close to control levels. For the other four delay intervals, there was a 17% or 18% reduction in matching accuracy across the dose range.

Discriminability

The values of Pw, Px, Py, and Pz were summed across birds for each delay interval and dose level. For the 0.5-mg/kg dose, there were no misses (Px) or false alarms (Py) at the 0-s delay interval. When Px or Py is zero, or when both values are zero, the discriminability index cannot be calculated. In this case, one response was added to the zero values. Equation 1 was used to calculate an estimate of discriminability (log d) for each delay and dose level. The best fitting negative exponential functions for the discriminability values for each dose level are shown in Figure 4. Values for the initial discriminability, log d_0, the rate of forgetting, b, and variance accounted for (VAC) are shown for each dose level. In all cases the negative exponential function provided a close fit to the data with the variance accounted for by the functions being 90% or more. The value for the initial discriminability, log d_0, remained at the control level for the 0.5-mg/kg dose, then decreased as the dose increased, particularly at the 12.5-mg/kg dose. The value for the rate of forgetting, b, increased systematically up to the 5.0-mg/kg dose, where the value remained stable.

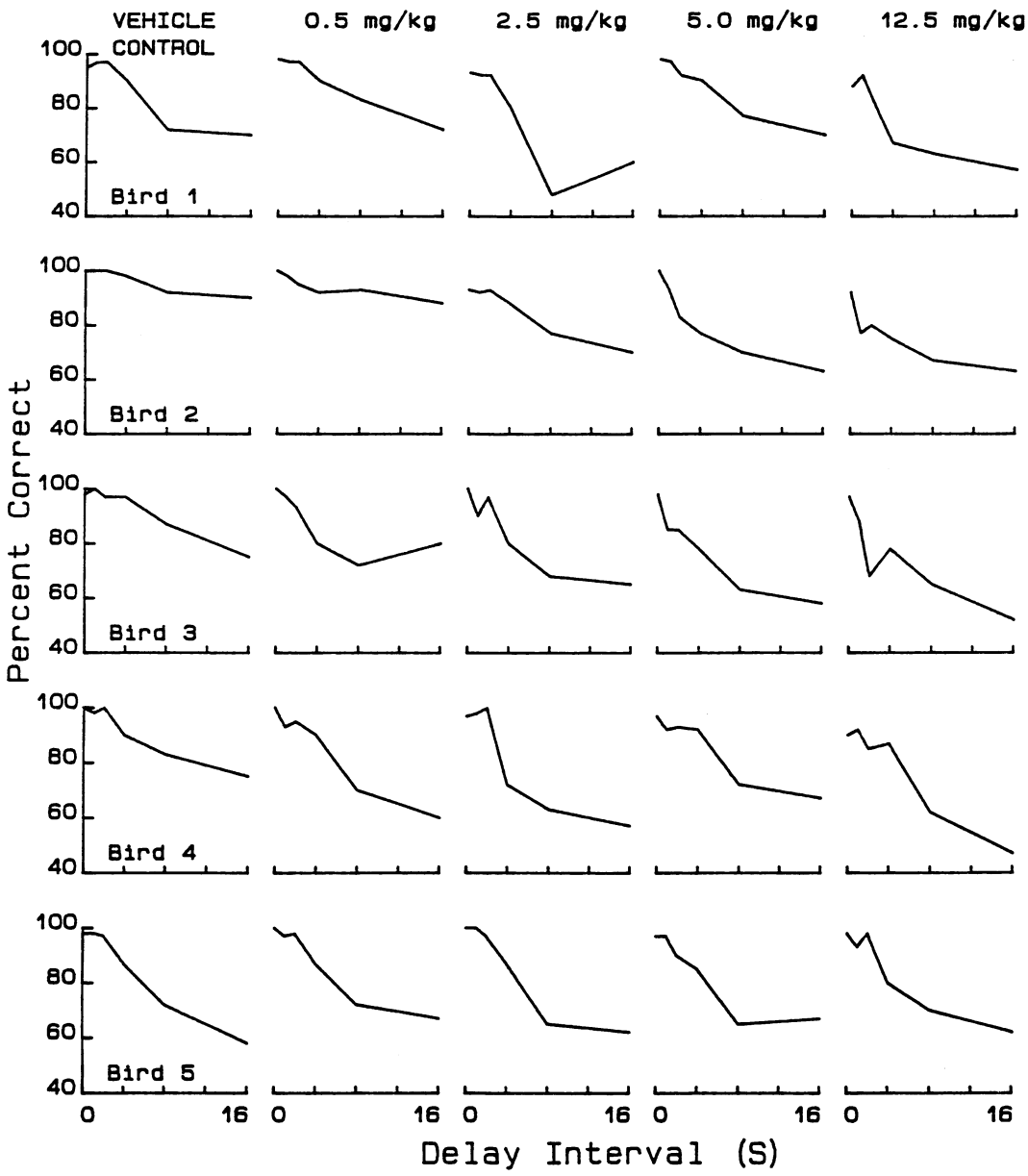

Fig. 2. Mean percentage correct for each bird across the six delay values for each drug condition.

Discriminability estimates were also calculated for each individual bird. At the shorter delay intervals, there were a number of cases in which either Px or Py was zero or both values were zero. When this occurred one response was added to the zero values. This meant that a value for discriminability could be calculated at each delay interval for each bird across the dose levels. The best fitting negative exponential function was calculated for the log d values for each dose level for each of the 5 birds. The negative exponential function provided a close fit to the log d values for the individual birds. The functions accounted for 75% to 98% of the variance with a mean of 89%.

The initial discriminability, log d_0, and rate of forgetting, b, values for each bird as a func-

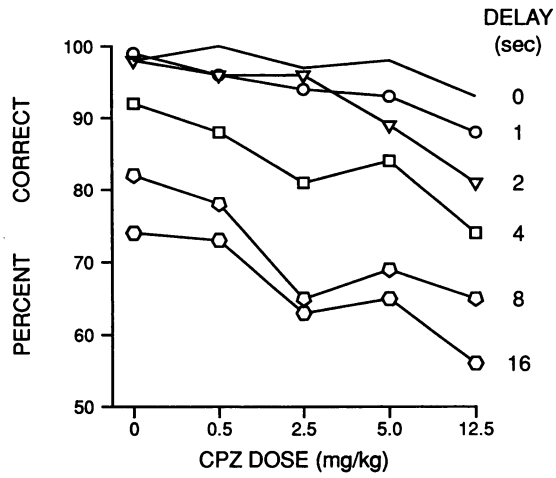

Fig. 3. Group-mean percentage correct for each delay interval as a function of drug dose.

tion of the dose of CPZ are presented in Figure 5. For 4 of the 5 birds there is a consistent pattern of changes in the values for log d_0 and b across the drug doses. For Birds 1 through 4 the log d_0 values decreased and the b values increased with increasing drug dose. For Birds 1 and 2 the log d_0 values did not decrease substantially until the 12.5-mg/kg condition. The log d_0 values for Bird 3 decreased systematically until the 12.5-mg/kg condition, in which the value was slightly greater than for the 5.0-mg/kg condition. The log d_0 value for Bird 4 did not decrease substantially until the 5.0-mg/kg condition. Although there is variability across the doses, for Birds 1 through 4 the value of log d_0 is consistently lower for the 12.5-mg/kg CPZ dose than for the control condition.

For Birds 1 through 4 the values for the rate of forgetting, b, also showed variability across the drug conditions, but for all birds the b value for the 12.5-mg/kg condition was higher than for the control condition. The increase in b in the 12.5-mg/kg condition was extremely large for Bird 3. Bird 5 showed little change in log d_0 or b values across the drug doses, apart from a decrease in log d_0 in the 5.0-mg/kg condition.

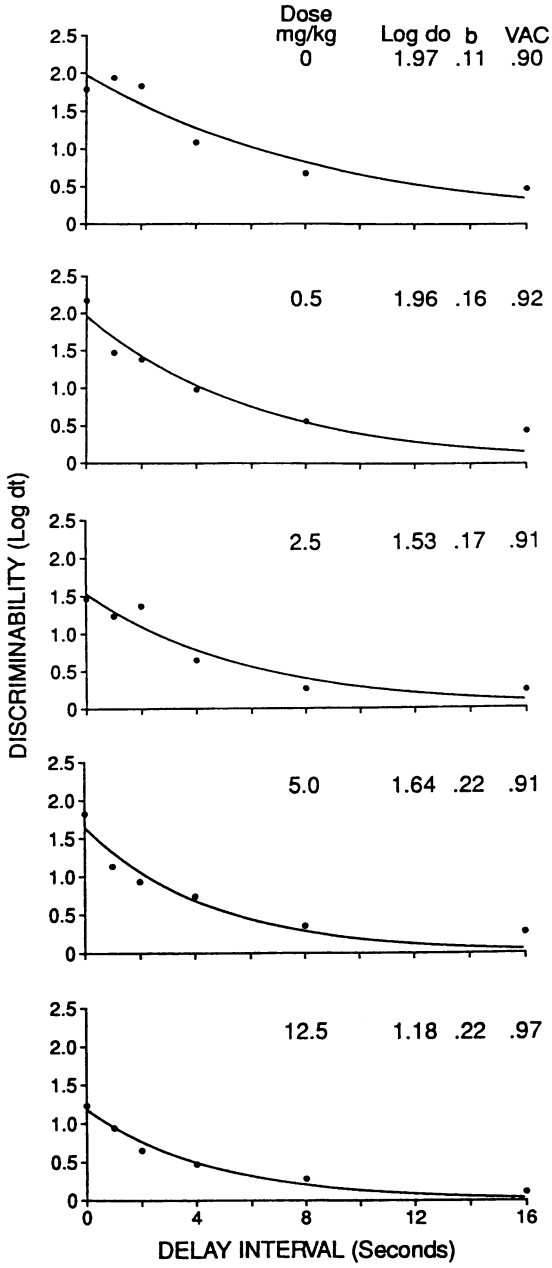

Fig. 4. Log d values from the group data plotted for each delay and drug dose. The smooth curves are negative exponential functions with parameters log d_0 and b. VAC, variance accounted for.

Effects of CPZ on Latency Measures

For each session, the median center- and side-key latency for the 20 trials at each of the six delay intervals was calculated. The mean of these medians gave a mean center- and side-key latency for each subject at each delay for each drug dose. These data were submitted to an analysis of variance using the GENSTAT® statistical package with delay, dose, and key as factors. Because the latency data were not

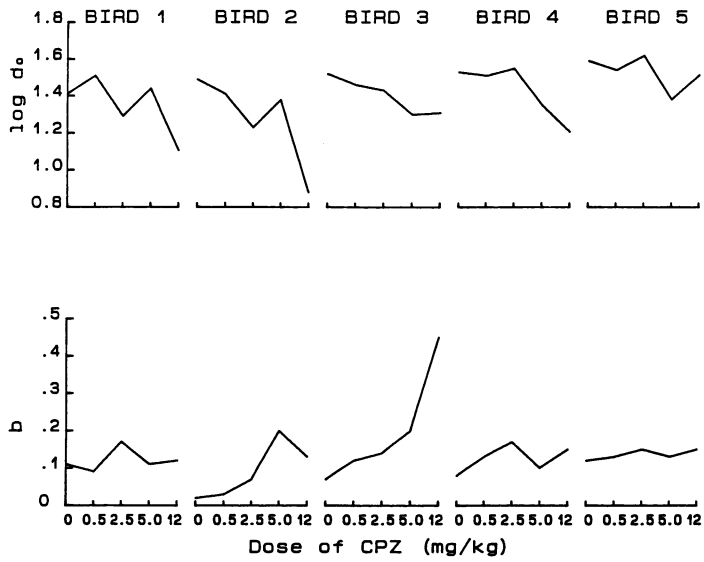

Fig. 5. Values for initial discriminability, log d_0 (top panel), and rate of forgetting, b (bottom panel), as a function of drug dose for each bird.

normally distributed, they were logarithmically transformed prior to the analysis of variance. The center- and side-key latency measures showed different linear functions resulting from increasing delay—linear trend: $F(1, 20) = 8.14, p < .05$. The side-key latency measure increased at a significantly greater rate with increasing delay than did the center-key latency measure. There was no statistically significant effect of dose on the latency measures, $F(1, 100) = 2.52, p > .05$.

Because there was no significant effect of dose on latency measures, data were pooled across the dose levels. The mean center- and side-key latency measures for each delay interval for each bird are shown in Table 1. Latency data for the individual birds are presented in Appendix B.

DISCUSSION

In this study, the effects of five doses of CPZ on the DMTS performance of pigeons were quantified using the exponential model of remembering. Chlorpromazine produced markedly different effects on the parameters of initial discriminability, log d_0, and the rate of forgetting, b. The parameters obtained from the analysis of the group data (Figure 4) showed that there was no difference in the log d_0 values for the vehicle control condition and the lowest CPZ dose (0.5 mg/kg). A decrease in the log d_0 values was found for the 2.5-mg/kg condition, with a further substantial decrease at the highest dose (12.5 mg/kg). The values for the rate of forgetting, b, showed an increasing trend as the dose increased.

The same pattern of results was found in the analysis of changes in log d_0 and b values for individual birds. Figure 5 shows that, for all but Bird 5, log d_0 values decreased and b values increased as the dose of CPZ increased.

In terms of the behavioral processes affected by the drug, the results show that CPZ affected both discrimination and memory or retention processes. The functions for the group data suggest that memory or retention processes were being affected at a lower dose than were discrimination processes (i.e., 0.5 mg/kg compared to 2.5 mg/kg). However, the parameters obtained for individual birds do not show such clear dose-dependent effects of CPZ on log d_0 and b.

These conclusions concerning the effects of CPZ on discrimination and memory processes are consistent with the pattern of changes in the percentage correct data for both the individual subjects and the group means. For the individual-subject percentage correct data (Figure 2), changes in the slope of the percentage correct functions are apparent with increasing doses of CPZ. There are also de-

Table 1

Mean center and side key latency (in seconds) at each delay interval for each bird.

	Center-key latency					Side-key latency				
	Subject					Subject				
Delay	1	2	3	4	5	1	2	3	4	5
0	2.72	2.46	2.83	2.11	2.73	1.38	1.26	1.15	0.99	176
1	2.56	2.53	2.91	2.07	2.79	1.49	1.46	1.17	0.86	1.65
2	2.63	2.47	2.89	2.13	2.79	1.50	1.43	1.33	1.05	1.72
4	2.62	2.46	2.92	2.15	2.73	1.43	1.49	1.36	1.15	1.80
8	2.68	2.35	2.94	2.14	2.80	1.35	1.46	1.42	1.27	1.80
16	2.66	2.54	2.90	2.07	3.16	1.35	1.73	1.60	1.33	1.69

creases in performance at the short delay values with increasing drug dose for all birds except Birds 3 and 5. The group means in Figure 2 show that there is a greater decrease in performance at the 4-, 8-, and 16-s delay intervals than there is at the short delays, again suggesting changes in memory or retention processes. In addition, the decreases in performance at short delay intervals that did occur indicate that the drug also affected discrimination processes. It is unlikely that this pattern was caused by a simple ceiling effect in the data, because in most cases performance was well below 100%.

The findings of this study are not in agreement with the conclusion reached by Heise and Milar (1984) in an extensive review of drugs and stimulus control. These authors argued that conclusions from previous research—that drugs affect memory or retention processes—are erroneous due to a failure to examine the effects of different levels of control by predelay stimuli. Heise and Milar concluded that at least for scopolamine, sodium amobarbital, ethanol, and chlordiazepoxide, decreases in accuracy on delayed discrimination tasks were not caused by changes in memory or retention processes. This does not appear to be the case for the effects of CPZ, under which there was a clear change in the rate of forgetting, b.

It is interesting to note that CPZ caused a decrease in accuracy of DMTS performance at doses that did not significantly change the center- or side-key latency measures. These measures were used as an index of psychomotor performance or overall rate of responding. In a previous study using monkeys, Glick et al. (1969) found that accuracy on a delayed matching task was not impaired unless there was an accompanying decrease in the response rate. In the present study there was no increase in the latency measures with increased drug dose, despite the changes in the accuracy of matching performance. It is unclear why the relationship between matching accuracy and psychomotor performance found in this study differed from that reported by Glick et al. (1969), although it may be due to interspecies differences.

The exponential model of remembering accounted well for the data in this study. The variance accounted for by the function for both the individual-bird and group data was high. It has been proposed that the parameters log d_0 and b are theoretically independent, and there is experimental evidence to support this contention (White, 1985). A recent study using the exponential model of memory to quantify the effects of scopolamine found that drug-induced changes in the two parameters supported this contention (Kirk et al., 1988). In the present study there is less support for the notion that these two parameters are independent, but the results did show that, on average, changes in the rate of forgetting occurred at a dose lower than that which lowered initial discriminability.

In conclusion, behavioral pharmacology as a discipline has been criticized recently for having moved away from an analysis of the behavioral mechanisms of drug action (Branch, 1984), and as a result having few general principles and no general theory (Heise & Milar, 1984). The results of the present study suggest that two recent advances in the experimental analysis of behavior—the behavioral model of signal detection (Davison & Tustin, 1978) and the subsequent development of the exponential model of remembering (White, 1985)—have the potential to overcome this criticism.

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APPENDIX A

Numbers of correct responses at each delay for each drug condition and for each stimulus, for Birds 1 through 5. Data are summed over three sessions, 10 trials per color per session; maximum score = 30.

	Green sample						Red sample					
	Delay (s)						Delay (s)					
	0	1	2	4	8	16	0	1	2	4	8	16
Saline												
Bird 1	29	28	30	28	21	20	28	30	28	26	22	22
2	30	30	30	29	28	25	30	30	30	30	27	29
3	30	30	30	30	26	19	29	30	28	28	26	26
4	30	30	30	28	27	22	30	29	30	26	23	23
5	29	29	29	24	19	12	30	30	29	28	28	23
0.5 mg/kg CPZ												
Bird 1	30	29	30	27	25	20	30	29	28	27	25	23
2	30	29	28	27	28	25	30	30	29	28	28	28
3	30	29	30	26	24	24	30	29	26	28	19	24
4	30	27	28	25	22	19	30	29	29	29	20	17
5	30	28	30	24	24	21	30	30	29	28	19	19
2.5 mg/kg CPZ												
Bird 1	27	25	25	20	4	8	29	30	30	28	25	28
2	30	29	28	29	27	22	26	26	28	24	9	20
3	30	30	30	29	24	21	30	24	28	19	17	12
4	28	29	30	15	19	14	30	30	30	28	20	18
5	30	30	29	27	25	23	30	30	29	25	14	14
5.0 mg/kg CPZ												
Bird 1	30	30	29	26	22	20	29	28	26	28	24	22
2	30	29	25	27	24	21	30	27	25	19	18	17
3	29	27	29	27	22	17	30	24	22	20	16	18
4	28	29	27	28	25	20	30	26	29	27	12	20
5	28	28	25	22	15	18	30	30	29	29	24	22
12.5 mg/kg CPZ												
Bird 1	24	25	21	11	10	8	29	30	29	29	28	27
2	27	19	21	20	18	18	28	27	27	25	22	20
3	28	28	26	21	21	19	30	25	15	16	18	12
4	25	25	22	25	16	12	29	30	29	28	21	16
5	29	27	29	24	25	20	30	29	30	24	17	17

APPENDIX B

Mean center- and side-key latency values (in seconds) for each bird at each delay and drug condition.

	Center-key latency						Side-key latency					
	Delay (s)						Delay (s)					
	0	1	2	4	8	16	0	1	2	4	8	16
Saline												
Bird 1	2.12	2.08	2.40	2.20	2.28	2.32	1.33	1.48	1.53	1.52	1.37	1.52
2	2.37	2.37	2.32	2.33	2.40	2.32	1.18	1.33	1.35	1.40	1.45	1.48
3	2.80	1.76	2.80	2.80	2.80	2.70	1.35	1.28	1.40	1.53	1.53	1.72
4	2.17	1.92	2.20	2.03	2.13	2.10	0.90	0.90	0.93	0.97	1.10	1.15
5	2.97	2.90	2.95	2.85	3.05	4.90	1.92	1.72	1.70	1.83	2.08	1.68
0.5 mg/kg CPZ												
Bird 1	2.70	2.50	2.70	2.60	2.60	2.62	1.30	1.40	1.43	1.43	1.38	1.22
2	2.20	2.30	2.27	2.40	2.20	2.30	1.15	1.17	1.38	1.33	1.38	1.55
3	2.80	2.90	2.85	2.95	2.98	2.90	1.18	1.15	1.30	1.25	1.37	1.70
4	1.90	1.97	1.97	2.20	1.97	1.92	1.02	1.02	0.90	1.13	0.98	1.05
5	2.90	3.15	2.90	2.70	2.75	2.80	1.65	1.77	1.95	2.18	1.75	1.85
2.5 mg/kg CPZ												
Bird 1	3.10	2.90	2.90	2.85	3.05	3.10	1.37	1.42	1.62	1.48	1.27	1.23
2	2.45	2.57	2.67	2.28	2.30	2.72	1.23	1.37	1.23	1.38	1.38	1.65
3	2.70	2.85	2.87	2.78	2.70	2.70	1.12	1.08	1.27	1.37	1.43	1.35
4	2.17	2.10	2.25	2.17	2.30	2.10	0.97	1.07	0.90	1.07	1.20	1.18
5	2.77	2.62	2.87	2.70	2.72	2.60	1.68	1.55	1.70	1.67	1.85	1.88
5.0 mg/kg												
Bird 1	2.15	2.05	2.00	2.17	2.20	2.05	1.17	1.40	1.32	1.25	1.33	1.22
2	2.20	2.10	2.10	2.10	2.00	2.23	1.23	1.43	1.57	1.58	1.40	1.65
3	2.90	2.97	2.95	3.05	3.05	3.05	1.10	1.17	1.28	1.33	1.43	1.58
4	2.15	2.17	2.18	2.27	2.10	2.17	0.93	1.05	1.13	1.22	1.28	1.52
5	2.12	2.67	2.75	2.70	2.82	2.75	1.97	1.72	1.58	1.78	1.63	1.47
12.5 mg/kg												
Bird 1	3.53	3.25	3.15	3.27	3.25	3.22	1.75	1.73	1.62	1.48	1.38	1.55
2	3.10	3.30	2.97	3.20	2.85	3.15	1.52	1.98	1.63	1.78	1.70	2.32
3	2.95	3.07	3.00	3.03	3.15	3.15	0.98	1.18	1.40	1.32	1.32	1.65
4	2.15	2.20	2.05	2.07	2.22	2.07	1.15	1.28	1.40	1.35	1.77	1.75
5	2.60	2.60	2.50	2.70	2.67	2.75	1.57	1.47	1.68	1.55	1.73	1.58