Effects of scopolamine on visual difference thresholds in the pigeon

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Two experiments using a psychophysical procedure were performed to examine the effects of scopolamine on visual discrimination performance in pigeons. The results of Experiment 1 showed dose-related increases in luminance difference thresholds, although performance at stimulus values well above threshold was unaffected by the drug. Experiment 2 extended the observations to the visual discrimination of line orientation. Dose-related increases in difference thresholds after scopolamine were again observed. However, performance was impaired to a similar extent at all stimulus values, which may indicate differences in the strength of stimulus control between the two experiments. The results provide further support for a discrimination-deficit hypothesis of anticholinergic action and emphasize the importance of using sensitive testing procedures in the analysis of complex drug effects.

The anticholinergic drug scopolamine disrupts performance in a wide range of experimental situations (Bignami, 1976; Longo, 1966). One common observation is that the drug increases levels of responding in situations in which responses would normally be suppressed (Carlton, 1969); thus, reported effects of scopolamine have included increased resistance to extinction (Hearst, 1959) and disruption of passive avoidance (Suits & Isaacson, 1968) and of habituation to a novel environment (Carlton & Vogel, 1965). On the basis of such observations, Carlton (1963) initially proposed that a central cholinergic system was involved in mediating the effects of nonreinforcement, and later extended the model to embrace a more general concept of response inhibition as a consequence of punishment, stress, or nonreward (Carlton, 1969). Such inhibition would then be disrupted by scopolamine.

However, it is not clear from many of the data cited by Carlton if the action of the drug is a specific disinhibition of responses, or if it impairs stimulus input mechanisms. As Warburton and Brown (1976) have pointed out, increases in nonrewarded responses may arise as a result of impaired discrimination between the stimuli determining the occasions for responding and nonresponding. In his extensive review, Bignami (1976) also acknowledges the importance of stimulus factors in the response changes produced by anticholinergics, postulating a drug-induced motor bias at some "interface" between the sensory and motor levels.

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Warburton and Brown (1971), using a discrete trial discrimination procedure, trained rats to leverpress in response to periodic increases in chamber illumination. Assessment of relative performance in trial and intertrial periods by means of a signal-detection analysis (Egan, Greenberg, & Shulman, 1961; Grier, 1971) showed a dose-related decrease in stimulus sensitivity under scopolamine with no systematic changes in response bias, that is, no specific response disinhibition.

As a test of the Carlton and Warburton hypotheses, Milar, Halgren, and Heise (1978) trained rats on a go/no-go discrimination involving two "go" stimuli and two "no-go" stimuli. They found that scopolamine increased responding on "no-go" trials but also decreased responding on "go" trials and reduced accuracy of discrimination between the two "go" stimuli, findings which are clearly at variance with a response disinhibition hypothesis.

Scopolamine-induced discrimination deficits have also been reported in cats (Bennett, Nunn, & Inman, 1971) and stump-tailed monkeys (Evans, 1975). However, Dews (1955) reported no effects of scopolamine on visual discrimination accuracy in pigeons, a result that has been replicated in this laboratory (Cleaves, Note 1).

It is known that strength of stimulus control (the degree to which behavior is controlled by a stimulus or stimulus complex) can profoundly modify the effects of drugs (Laties, 1975), and several investigations have indicated that behavior under strong stimulus control is less disrupted by scopolamine than is behavior under weak stimulus control (Laties, 1972; Laties & Weiss, 1966). Warburton (1974) found that groups of rats trained with a single relevant cue, either tone or light, were more impaired by scopolamine than were groups trained with a tone-light

combination. Indeed, further analysis of performance in the combined-cue group revealed a significant correlation between an individual's sensitivity to the drug and its dependency on a single cue, as shown by transfer tests. These results show differences in susceptibility to scopolamine, depending on the number of relevant stimuli. Overtraining has also been found to attenuate drug effects (Burešová, Bureš, Bohdanecky, & Weiss, 1964).

In the light of these findings, the absence of a scopolamine effect reported by Dews (1955) is not so surprising. Pigeons are extremely adept at visual discriminations. The distinctive color stimuli used by Dews would be unlikely to challenge his subjects' visual capabilities, and it seems reasonable to suggest that such a task would fail to reveal any but the most drastic reduction in discrimination capacity. Procedures which place a greater burden on the capacity of organisms to process stimulus information may, in consequence, prove more fruitful in the analysis of scopolamine effects.

Psychophysical methods have been used extensively to investigate visual processes in pigeons (Blough, 1958; Mentzer, 1966). The experiments to be reported here employed a psychophysical procedure for estimating visual difference thresholds in the pigeon (Hodos & Bonbright, 1972). Using this procedure, Hodos and Bonbright (1974) were able to demonstrate permanent luminance difference threshold elevations in pigeons with lesions of the nucleus opticus principalis thalami, where no deficit had been detected using standard brightness or pattern discrimination tasks (Hodos, Karten, & Bonbright, 1973).

Experiment 1 examined the effects of scopolamine on luminance difference thresholds. The procedure, a modified method of limits, permits not only the evaluation of difference thresholds on a particular dimension, but also the assessment of relative performance over a range of stimulus intensities within a single session. A drug-induced discrimination deficit would be expected to raise difference thresholds. In addition, if the drug has a differential effect at different levels of stimulus control, performance on the near-threshold trials of the series should be disrupted to a greater extent than performance on suprathreshold trials.

As a test of the generality of the stimulus processing hypothesis, Experiment 2 extended the observations to a different stimulus dimension, that of line orientation.

EXPERIMENT 1

Method

Subjects

Five adult feral pigeons (290-550 g) were used. Throughout the experiment, the subjects were maintained at 80% of their free-

feeding weights and given their total daily food requirement during experimental sessions.

Apparatus

The subjects were tested in a ventilated and sound-attenuated pigeon operant chamber with three 2.5-cm-diam translucent pecking keys aligned 2.5 cm apart in the front wall. A food well was situated under the center key; during reinforcement periods the well was illuminated and grain was made available.

The interior of the chamber was matte white and was illuminated by a fluorescent lamp mounted along the top of the rear wall behind a diffusing sheet of white translucent Perspex. Luminance, measured with an SEI photometer, varied from 54.4 cd/m² in the region of the lamp to 8.42 cd/m² in the region of the response keys.

The center key was illuminated by an externally located Kodak Carousel projector, with a 1.0-log-unit Kodak No. 96 Wratten neutral density filter permanently mounted in the path of the lamp (unregulated current), constituting the "standard" stimulus with a luminance of 5,305 cd/m². The current used was unregulated, as preliminary measurements showed that the light current fluctuations through the apparatus did not affect lamp luminance significantly. The variable stimuli consisted of a series of neutral density filters mounted in 5 × 5 cm slide holders. Filters of density values .8, .4, .2, and .1, providing 16%, 40%, 63%, and 80% transmission, respectively, were used. An additional filter was constructed from two sheets of microscope cover glass to provide a measured transmission of 89% (.05 density). Four identical sets of stimuli were made and randomly interchanged from session to session to insure against discrimination on the basis of spurious cues.

The left key was illuminated by orange light, and the right key by green, from diffused 2.9-W lamps.

Procedure

Pretraining. After the subjects had been trained to eat from the grain dispenser, they were shaped to peck the illuminated side keys, pecks to either being rewarded with 2-3 sec access to grain. The subjects were then trained to peck the center key when illuminated by the projector lamp. A single peck caused center key offset and side key onset; pecks to either side key were then rewarded. The response requirement on the center key was gradually raised to 10.

Discrimination training. A conditional discrimination procedure was then introduced such that left keypecks were rewarded only when the center key had been "bright" (no filter), and right keypecks were rewarded only when the center key had been "dim" (light attenuated by a .8-log-unit filter).

A session consisted of 60 trials of each stimulus presented in quasi-random fashion, with no more than three trials of the same stimulus occurring in succession. Initially, incorrect responses were followed by a 3.5-sec time-out period during which the house-lights were extinguished. A correction procedure was brought into operation with the previous stimulus repeated until a correct response was obtained (only the initial error was recorded for analysis). As learning progressed, the time-out period was discontinued but the correction procedure was maintained.

A 50% reinforcement schedule was introduced in order to maintain 80% body weight. On a random 50% of the trials, a correct response was reinforced with grain; on the other 50%, the food well was illuminated but no grain presented.

The 0 vs. .8 discrimination procedure was continued until a criterion of 90% correct on three consecutive sessions had been satisfied.

Threshold estimation. When the training criterion had been met, daily threshold estimations were begun. The first 10 trials of the session consisted of a practice period of 0 vs. .8, as in training. Data from this period were not used in the analysis. This was followed by a further 10 trials of 0 vs. .8, during which a criterion of 90% correct, that is, not more than one error, was set. If the criterion was not met, the rest of the session, a further 100 trials, continued as a training session. If the criterion was satisfied, the psychophysical procedure was carried out with the 0 vs. .8 trials

being followed by four further 10-trial periods of 0 vs. .4, 0 vs. .2, 0 vs. .1, and 0 vs. .05, respectively.

This ascending series was immediately followed by a second in exactly the same manner, including a second 10-trial practice period with 0 vs. .8. The data for the two series were combined to give measures of percent correct for each stimulus pair, from which difference thresholds could be estimated. In the present case, the difference threshold is defined as the difference between the standard stimulus and that stimulus value giving rise to a score of 75% correct, that is, midway between no discrimination and perfect discrimination. Where the 75% point did not correspond exactly with one of the stimulus values, the difference threshold was estimated by linear interpolation.

To ensure a stable predrug baseline, data were collected daily for each subject until there occurred a run of five consecutive sessions in which the individual thresholds did not deviate from their mean by more than 25%.

Injections. Treatments consisted of three doses of scopolamine hydrobromide (.025, .05, .1 mg/kg), a saline control, and .1 mg/kg of scopolamine methylbromide, a quaternary anticholinergic which does not enter the CSN to any great extent and can therefore be used as a control for the effects of peripheral cholinergic blockade.

Drugs were dissolved in saline and administered by injection into the pectoral muscle 15 min before the start of a session. Each subject received all doses in randomized series, birds 101 and 106 receiving two series and Birds 102, 103, and 105 receiving three. A minimum of two sessions was given between drug treatments provided that, by the second day, thresholds were within the baseline range.

Results

All subjects achieved the criterion of stability for difference thresholds in 8-16 sessions. Mean difference thresholds ranged from .065-.124 density, representing luminance differences of 13.9%-24.8% (Table 1). It is of interest to note that, although the standard stimulus used by Hodos and Bonbright (1972) was 1.2 log units less intense than that used in the present experiment, these authors obtained very similar threshold differences (group mean: .125 density, i.e., 25% luminance difference) consistent with Weber's law. (The Weber fraction for Hodos and Bonbright was .25; for the present data it was .20.)

Figure 1 depicts the mean psychometric function for each subject over the last five baseline sessions. Percentage correct is plotted as a function of density difference, each point representing the mean of 100 trials.

Table 1
Mean Luminance Difference Thresholds
for the Last Five Baseline Sessions

Subject	Difference Threshold		Percent*
	Mean	Range	
101	.105	.131-.079	21.5
102	.124	.155-.093	24.8
103	.067	.084-.050	14.3
105	.065	.081-.049	13.9
106	.118	.148-.088	23.8
Mean	.096		19.7

Figure 1. Mean psychometric functions for each subject and for the group, plotted over the last five baseline sessions (Experiment 1).

Mean luminance difference thresholds for the drug treatments are shown in Figure 2.

In all subjects, with the exception of 105, an orderly relationship between drug dose and threshold can be seen.

A treatment $\times$ subjects analysis of variance indicated a significant effect of drug treatments on difference thresholds [$F(4,16) = 4.34$, $p < .025$]. A test for linear trend (excluding methylscopolamine scores) was highly significant [$F(1,12) = 9.74$, $p < .01$]. Comparisons between treatments using the Newman-Keuls test, indicated that the highest dose of scopolamine (.1 mg/kg) produced significantly higher difference thresholds ($p < .05$) than the .025-mg/kg dose and the saline control. Thresholds under methylscopolamine did not differ significantly from the control condition, indicating that the peripheral actions of the drug, for example, mydriasis, made no significant contribution to the effects observed.

The percentage of errors made at each filter value under drug treatments was submitted to a two-way analysis of variance which revealed significant main effects of filter ($p < .001$) and drug ($p < .01$) and a significant interaction between these factors ($p < .01$).

Inspection of Figure 3, which compares psychometric functions for the saline and .1 scopolamine conditions, suggests that the interaction can best be accounted for by a greater disruption of performance under scopolamine at the lowest density difference than at the highest density difference. The Scheffé

Figure 2. Mean luminance difference thresholds for each subject and for the group after drug treatment (Experiment 1).

Figure 3. Mean psychometric functions for saline (solid line) and .1 mg/kg scopolamine (dashed line) conditions (Experiment 1).

test for pairwise comparisons of means showed a significant difference between saline and .1 scopolamine at .05 density ($p < .05$) but no difference at .8 density, thus lending support to this interpretation.

These results support the impaired stimulus discrimination hypothesis of scopolamine action. The difference in luminance between two stimuli necessary for discrimination was greater under scopolamine. In addition, the effects of the drug were found only where discrimination was most difficult, the easier discriminations within the same session remaining resistant to disruption.

In order to test the generality of these findings, a second experiment was carried out employing a different stimulus dimension.

EXPERIMENT 2

Method

Subjects

A different group of five adult feral pigeons was used and maintained in the same manner as those in Experiment 1.

Apparatus

The apparatus was that used in Experiment 1. The stimuli consisted of grids of black lines (1 mm thick, spaced 1 mm apart) of differing orientation, drawn on white translucent paper and mounted in 5 × 5 cm slide holders. When projected onto the center key, each grid displayed six lines, with the first and last lines coinciding with the edges of the key in order to eliminate bright segments which may have provided subjects with additional cues.

Procedure

Discrimination training. After pretraining, the subjects were trained on a conditional discrimination procedure essentially the same as in Experiment 1 but with left keypecks rewarded when the stimulus orientation was vertical (0 deg) and right keypecks rewarded when the orientation was horizontal (90 deg).

The stimulus series used in psychophysical testing was as follows: 0 vs. 90 deg, 0 vs. 60 deg, 0 vs. 45 deg, 0 vs. 30 deg, 0 vs. 15 deg. Daily thresholds were obtained until the criterion of stability had been achieved.

Injections. In this experiment preliminary tests revealed a tendency to pause for extended periods or cease responding altogether under .1 mg/kg scopolamine. Thus, treatments consisted of 0, .025, .05, and .075 mg/kg scopolamine and .075 mg/kg methylscopolamine control. Birds 104, 107, 108, and 110 received each dose once, and Bird 111 received each dose twice in randomized sequence. Each drug session was followed by a minimum of two nondrug threshold estimations.

Results

Subjects achieved the criterion of stability for difference thresholds in 9-25 sessions. Mean difference thresholds are presented in Table 2.

Table 2
Mean Orientation Difference Thresholds
for the Last Five Baseline Sessions

Subject	Difference Thresholds (in Degrees)	
	Mean	Range
104	11.3	14.1- 8.5
107	12.5	15.6- 9.4
108	16.1	20.1-12.1
110	23.2	9.0-17.4
111	35.3	44.1-26.5
Mean	19.7

Figure 4. Mean psychometric functions for each subject and for the group, plotted over the last five baseline sessions (Experiment 2).

Figure 5. Mean orientation thresholds for each subject and for the group after drug treatment (Experiment 2).

Figure 4 depicts the mean psychometric function for each subject over the last five baseline sessions. Percent correct is plotted as a function of orientation difference, each point representing the mean of 100 trials.

During the course of this experiment, slight shifts in baseline thresholds became apparent in four subjects, two showing increases and two showing decreases. To allow for this, thresholds after drug treatments are expressed as a percentage of a moving mean computed for the last five nondrug sessions prior to that drug session (Figure 5).

A treatments $\times$ subjects analysis of variance indicated a significant effect of drug on difference thresholds [$F(4,16) = 3.52$, $p < .05$]. A test for linear trend was significant at the .05 level. Individual comparisons of treatment means showed a significant difference ($p < .05$) between .075 scopolamine and saline. Thresholds under methylscopolamine did not differ significantly from the control condition.

A two-way analysis of variance of percent errors at each stimulus value under each dose of drug revealed significant effects of drug ($p < .025$) and stimulus ($p < .001$) but, in contrast to Experiment 1, no interaction between these factors. This suggests that the drug was impairing performance comparably at all stimulus values, and this suggestion was borne out by visual inspection of the data.

DISCUSSION

Warburton (1975) has advanced the hypothesis that a cholinergic system is involved in the processing of stimulus information by modulating the signal-to-noise ratio in sensory pathways. Such a model predicts certain parallels between the effects of scopolamine and changes in the distinctiveness of discriminative stimuli. Evans (1975) carried out a detailed analysis, in the stump-tailed monkey, of the relationship between distinctiveness (luminance) of stimuli and a number of behavioral measures such as probability, latency, and accuracy of responding. The effects of scopolamine were found to resemble the pattern of effects produced by reducing discriminability of stimuli in undrugged animals.

The present experiments sought to extend these findings by examining scopolamine effects on visual difference thresholds in the pigeon. The results of Experiment 1 showed the predicted increases in luminance difference thresholds under scopolamine, that is, the drug-impaired subject's ability to discriminate small differences in stimulus luminance. It was further predicted that performance at near-threshold stimulus values would be disrupted to a greater extent than performance at stimulus values well above threshold. The interaction between dose of scopolamine and stimulus intensity in Experiment 1 suggests just such a differential effect; the highest dose,

while significantly disrupting overall performance, had no significant effect at the highest stimulus value. This is in keeping with previous studies which have indicated that strong stimulus control can attenuate the disruptive effects of scopolamine (Laties, 1972; Laties & Weiss, 1966).

To test the generality of the findings of Experiment 1, Experiment 2 examined the effects of scopolamine on orientation difference thresholds. The results show dose-related increases in thresholds but no drug $\times$ stimulus interaction, performance being equally impaired at all stimulus values.

Examination of the data suggests that the line orientation discrimination was more difficult than the luminance discrimination. Subjects required a greater number of trials to criterion on both initial acquisition and threshold stability. In addition, baseline thresholds continued to shift throughout the course of the experiment. These considerations suggest the possibility that responding was under weaker stimulus control at the start of drug testing in Experiment 2, and hence more vulnerable to scopolamine. If such were the case, overtraining on the initial discrimination task and a longer period for assessing threshold stability might promote the differential pattern of scopolamine disruption seen in Experiment 1.

Thus, the present study shows clear visual discrimination deficits in pigeons due to scopolamine. Previous studies have shown a scopolamine-induced disruption of fixed interval responding (Laties & Weiss, 1966) and counting schedules (Laties, 1972) but not color discrimination (Dews, 1955). The most likely explanation for the latter finding is that the simple color stimuli employed were not a sufficient test for discrimination impairment, any visual capability remaining after scopolamine treatment still being sufficient to make an accurate discrimination. The impairments found in the present study serve to emphasize the value, for assessing anticholinergic drug effects, of testing subjects at the limits of their capacity for processing stimulus information.

Response inhibition played no significant part in these experiments, since a response was required on every trial, and it is difficult to see how explanations based on response factors could account for the pattern of effects obtained. However, in a recent series of studies designed specifically to test scopolamine effects on response inhibition, Gonzalez and Altshuler (1979) found normal development of a conditioned emotional response (the suppression of ongoing appetitive behavior in the presence of an aversive stimulus). Furthermore, in a discriminated DRL (differential reinforcement of low rates of responding) task with a separate response lever for each component, they found no disruption of DRL responding per se but did find reduced discrimination accuracy.

These findings and those of Milner et al. (1978) thus call into question the validity of the response disinhibition hypothesis.

The pigeon has been much used in the study of discriminative control of behavior. Its well developed visual capacities and suitability for operant procedures should therefore make it an obvious choice for the investigation of drug effects on discrimination. The present experiments, using a sensitive psychophysical procedure, demonstrated scopolamine-induced discrimination deficits which were not apparent when using more conventional discrimination procedures (Dews, 1955, 1957). Furthermore, using the same procedure, increases in difference thresholds were found along two different stimulus dimensions.

These data thus provide an important extension of Warburton's (1975) hypothesis that a central cholinergic system mediates the stimulus control of behavior.

REFERENCE NOTE

1. Cleaves, L. Unpublished findings, 1978.

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