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# The Effects of Scopolamine and Cues to Forget on Pigeons' Memory for Time[1]

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SANTI, A. AND S. BRIDSON. *The effects of scopolamine and cues to forget on pigeons' memory for time.* PHARMACOL BIOCHEM BEHAV **39**(4) 935–940, 1991.—Pigeons were trained with a 0-s delayed symbolic matching-to-sample procedure to indicate whether a houselight sample stimulus was short (2 s) or long (8 s) by pecking a red or a green comparison stimulus. In Experiment 1, the pigeons received injections of scopolamine hydrobromide (0.015 mg/kg), or saline, and the delay interval was manipulated (0, 1, 3, and 9 s). Memory for time was significantly poorer following scopolamine injections than following saline injections. A significant choose-short bias was observed under scopolamine at delays as brief as 3 s, but not under saline. In Experiment 2, a brief postsample cue (a vertical or horizontal line) signaled whether the comparison stimuli would be presented or omitted on each trial. During training, comparison stimuli were always presented following the remember (R) cue, but never following the forget (F) cue. During testing, memory for time was significantly poorer on F-cue trials than on R-cue trials. A significant choose-short bias was observed on F-cue trials at the 5- and 10-s delays, but not on R-cue trials. The results suggest that anticholinergic blockade accelerates the rate at which memory for temporal events is foreshortened in working memory. This effect is similar to that produced by an explicit cue to forget the temporal sample.

Scopolamine Delayed matching-to-sample Pigeons Temporal memory Time Directed forgetting Working memory Anticholinergic

THE effects of anticholinergic drugs on memory have been assessed in a variety of species (humans, monkeys, chimpanzees, rats, mice, pigeons) with a variety of tasks (passive and active avoidance, spontaneous alternation, radial arm maze, delayed matching-to-sample and various discrimination learning tasks). This research has demonstrated that, in small rodents, anticholinergic drugs produce deficits in radial-arm maze performance (9, 48, 54), which appear to be greater for the working memory component of this task than for the reference memory component (3, 24, 35, 58). Reference memory is regarded as a relatively stable knowledge base concerning which response to make for particular stimulus sequences, which outcomes follow certain responses, and so on. Working memory is regarded as maintaining a limited amount of trial-specific information over relatively brief time periods. The greater sensitivity of working memory to anticholinergic effects has also been reported for rats in water navigation tasks (5,56), for pigeons in delayed matching-to-sample tasks (38–40), and for humans on tests of anterograde and remote memory (52). Working memory performance of rhesus monkeys has also been disrupted by anticholinergic agents (1, 2, 4, 33). Despite the frequently reported enhanced sensitivity of working memory to cholinergic blockade, there have been a few reports of equivalent anticholinergic effects on reference memory (16,30), especially when higher doses of anticholinergics are used (5,40).

The enhanced sensitivity of working memory processes to cholinergic blockade would lead one to expect that these effects should be delay-dependent. That is, the effect of a particular anticholinergic agent or of increasing doses of the agent should be greater at long than at short delay intervals. For monkeys, delay-dependent impairments of anticholinergics on delayed matching-to-sample have been obtained in several studies (2, 33, 34), with only one exception (10). However, there are only two reports of delay-dependent effects for rats (32,53). Most frequently, when rats are tested on a variety of delayed response tasks, anticholinergics like scopolamine produce a generalized disruption of performance which is equivalent across short and long delays (7, 8, 11, 17–19, 21, 23, 42, 55). Similarly, in pigeons tested on delayed matching-to-sample, the effects of scopolamine have uniformly been delay-independent (38–40, 51). The ubiquitous finding of delay independence suggests either that the notion of cholinergic blockade specifically affecting working memory processes is wrong or incomplete, or that the tasks used in these studies are not sensitive enough to detect delay-dependent effects.

In almost all of the tasks used to examine the effects of anticholinergics on animal memory, the events to be remembered have been particular types of visual stimuli, auditory stimuli, or spatial locations. The nature of the memory representation for these stimuli may be different from those for other stimuli, such as event durations. That is, while the memory code for various visual, auditory and spatial stimuli may be categorical in nature, the memory code for event durations appears to be analogical. Support for this idea comes from recent research on pigeons' memory for event duration. Pigeons have been trained to indicate whether a sample is short (2 s) or long (8 s) by pecking a

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red or a green comparison stimulus for reinforcement. This research has demonstrated that, when the delay interval between termination of the sample and the onset of the comparison stimuli is increased, a choose-short response bias is evident (22, 43, 44, 47). That is, pigeons respond to the long sample duration after a long delay interval as if it had been the short duration. It has been proposed (47) that the pigeons' subjective representation of the event duration in working memory becomes systematically shortened during the delay interval. As a result, after a long delay interval, the remembered duration of the long sample is more similar to the actual duration of the short sample. Recently, there has been converging evidence supporting the hypothesis that the memory code for event durations is analogical rather than categorical (45,57).

Both d-amphetamine (50) and tetrahydrocannabinol (6) have been shown to reduce the accuracy of temporal discrimination performance in pigeons. In both studies, increased doses of the drugs produced an increase in the choose-short response bias at a 0-s delay. However, a recent study (46) has reported that d-amphetamine produces a choose-long response in pigeons at a 0-s delay. This finding is more consistent with the hypothesis that amphetamines lengthen perceived time and with the findings that methamphetamine produces overestimation of time intervals in rats (28,29).

The purpose of the present research was to examine the effects of scopolamine on pigeons' memory for time (Experiment 1) and then to compare these effects to those produced by giving the pigeons an explicit signal to forget the sample stimulus (Experiment 2).

## EXPERIMENT 1

### METHOD

*Subjects*

Twelve adult male White Carneaux pigeons, maintained at approximately 80% of their ad lib weight and housed individually with constant access to grit and water, served as subjects. Fluorescent lights were illuminated on a 12:12 light/dark cycle in the colony room. All birds had extensive experience with delayed matching tasks including memory for event duration. However, this was the first study in which the effect of scopolamine was examined on memory for event durations.

*Apparatus*

Four Coulbourn modular operant test cages (Model #E10-10), housed individually in isolation cubicles (Model #E10-20), were used. Each cubicle was equipped with a ventilation fan and baffled air intake and exhaust system. Each test cage was equipped with three horizontally aligned, clear plastic keys behind which projectors could display stimuli (red or green field, or a black dot on a white background) onto a frosted rear projection screen (Coulbourn Model #E21-18). Directly below the center key was a 5.7 × 5-cm opening that provided access to a hopper filled with mixed grain (Coulbourn Model #E14-10). A houselight was located 6.5 cm above the center key and installed such that the light was directed upward to reflect from the top of the cage (Coulbourn Model #E11-01 with bulb #SL1819X). All experimental events and response measures were arranged and recorded by a microcomputer system (Motorola 6809 microprocessor) located in an adjacent room.

*Procedure*

All birds had received prior delayed matching training in which the sample stimulus was illumination of the houselight for 2 s (short) or 8 s (long). Sample duration varied randomly between trials with the constraint that the same duration occurred no more than four trials in a row. Termination of the sample was followed immediately (0-s delay) by presentation of red and green lights on the side keys as choice stimuli. Red was correct after a short sample and green was correct after a long sample for 6 of the birds. This relationship was reversed for the remaining birds. The position of the red and green lights on the side keys was counterbalanced over trials. A response to a side key terminated the choice stimuli and resulted in either 3 s access to mixed grain if correct or a 3-s blackout if incorrect. Following either reinforcement or blackout, an intertrial interval varying randomly between periods of 10–40 s was spent in darkness. Each session consisted of 72 trials. Prior to drug testing, the performance of all birds was above 90% correct matching.

On each session of drug testing, the birds received either an injection of saline or an injection of scopolamine hydrobromide at a dose of 0.015 mg/kg. This dose was selected because, in our previous work, it has produced reliable and selective effects on working memory (38–40). Larger doses disrupt both reference memory and working memory, as well as interfere with keypecking behavior generally. The drug was purchased from Sigma Chemical Co. (St. Louis, MO). All injections were made into the pectoral muscle 15–30 min prior to each test session in a volume of 1.0 ml/kg of body weight. One random order of the treatment conditions was used with the restriction that no more than two consecutive sessions could involve the same treatment. A total of 20 test sessions (10 saline, 10 scopolamine) were given. Each drug test session consisted of four blocks of twenty-four trials. Within each block of 24 trials, there were 9 short and 9 long samples tested at the 0-s delay, and 1 short and 1 long sample duration tested at delays of 1, 3, and 9 s. Consequently, the 0-s delay occurred randomly on 75% of the trials, and the three longer delays occurred randomly on 25% of the trials. This distribution of delays was used so that the reference memory of the sample durations and their associations with the comparison stimuli established during 0-s delay training would remain relatively stable (43). There was no illumination in the test chamber during the delay intervals. All other parameters were the same as those described previously.

### RESULTS AND DISCUSSION

The mean percentage correct matching performance during drug testing sessions at the four delay intervals is shown in Fig. 1. Accuracy was significantly lower with scopolamine than with saline, $F(1,11) = 51.57$, $p < 0.0001$, and it declined with increases in delay interval, $F(3,33) = 115.61$, $p < 0.0001$. Accuracy was also significantly higher on short-sample trials than on long-sample trials, $F(1,11) = 6.25$, $p < 0.05$. The analysis also revealed significant interactions of drugs by delay interval, $F(3,33) = 3.48$, $p < 0.05$, sample duration by delay interval, $F(3,33) = 4.20$, $p < 0.05$, and drugs by sample duration by delay interval, $F(3,33) = 6.91$, $p < 0.01$. For saline sessions, there was no significant difference in accuracy between short- and long-sample trials at any of the delays. However, for scopolamine sessions, accuracy on short-sample trials was significantly greater than on long-sample trials at the 3-s delay, $F(1,11) = 6.25$, $p < 0.05$, and at the 9-s delay, $F(1,11) = 14.34$, $p < 0.01$, but not at two shortest delays ($F < 1$). In addition, accuracy was significantly lower with scopolamine than with saline under all conditions except short-sample trials at the 9-s delay.

Significant choose-short effects were observed under scopolamine at delays as brief as 3 s, but not under saline. The absence of a choose-short effect under saline was probably due to

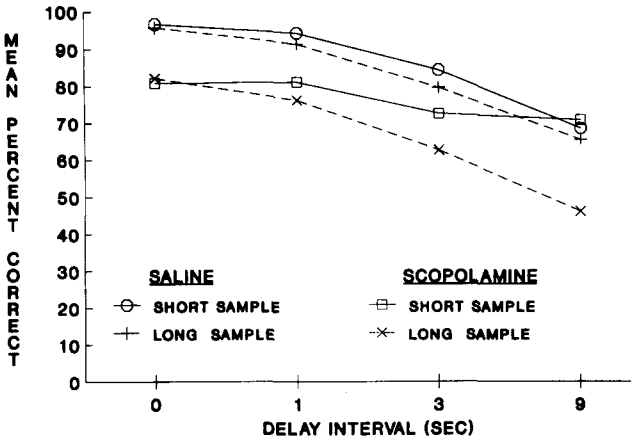


FIG. 1. Mean percent of correct matching responses as a function of scopolamine (0.015 mg/kg) or saline on short- and long-sample trials during testing at delays of 0, 1, 3, and 9 s.

the relatively short delay intervals that had been selected for this experiment in order to maximize sensitivity to the hypothesized effect of scopolamine. The choose-short effect is quite robust (21, 40–43, 52), and undoubtedly would have been evident on saline sessions if longer delay intervals had been used. Since numerous studies indicate that choose-short effects appear to be due to the subjective shortening of an analogical code (45, 47, 57), the present findings indicate that scopolamine accelerates the rate at which event durations are subjectively shortened in working memory. It is unlikely that scopolamine is simply making the pigeons forget the correct response. If it did just produce a general disruption of accuracy relative to saline, one would expect the scopolamine function to be lower than the saline function, but parallel to it. Scopolamine does disrupt accuracy relative to saline at the shortest delays, but the choose-short effect only emerges at the two longest delays under scopolamine. Additional support for the hypothesis of an accelerated rate of subjective shortening would be obtained if it could be shown that an explicit cue to forget the temporal sample stimulus produced the same effects as scopolamine.

## EXPERIMENT 2

To assess whether pigeons are capable of selectively maintaining information in working memory, researchers have used postsample cues to signal whether comparison stimuli will be omitted or presented on a particular trial. Following a remember or "R" cue, comparison stimuli are always presented, while following a forget or "F" cue, they are always omitted. By employing a probe-testing procedure in which comparison stimuli are infrequently presented after F cues, it has been shown that F cues control a lower level of matching accuracy than do R cues, which signal presentation of the comparisons (12, 14, 15, 20, 25–27, 36, 41). Similar effects have been obtained in studies with rats (13) and with squirrel monkeys (37). Studies have shown that F cues reduce accuracy more if they are presented early in the delay interval than if they are presented later in the delay (12,49). This indicates that F cues reduce accuracy by increasing the rate of forgetting, presumably because they reduce or halt postperceptual processing or rehearsal of the sample stimulus (12, 25, 36). In almost all of the directed forgetting research, both the samples and the R and F cues have been visual stimuli. Typically, colors have been used as sample stimuli, and line orientations have served as R and F cues. The purpose of this experiment was to obtain evidence that F cues accelerate subjective shortening of temporal information as scopolamine appeared to do in Experiment 1.

### METHOD

#### *Subjects and Apparatus*

The subjects and apparatus were the same as for Experiment 1.

#### *Procedure*

Following the testing described in the previous experiment, all birds were maintained in the colony room for approximately three weeks. Then they were given 4 sessions of event duration training with a 0-s delay. Each session consisted of 120 trials, and the other task parameters were the same as that described in Experiment 1. They then received 8 sessions of training in which the delay interval was increased to 1 s. In the next phase of training, termination of the temporal sample was followed by the presentation of a 1-s postsample cue (a vertical or horizontal line) on the center key. For half of the birds, the vertical line signaled the occurrence of comparison stimuli (R cue) and the horizontal line signaled their nonoccurrence (F cue). For the remaining birds, the cue functions were reversed. Red and green comparison stimuli were presented on the side keys immediately following termination of the R cue only. Each session consisted of 120 trials divided into 15 blocks of 8 trials each. Within each block of 8 trials, 4 R-cue and 4 F-cue trials were presented in a random order. All birds were given 23 sessions of directed forgetting training, and accuracy on R-cue trials was consistently above 90% correct for all birds on the last 4 sessions of training.

Each test session consisted of 120 regular trials, which were the same as during directed forgetting training, and an additional 24 probe trials. The 24 probe trials in each test session consisted of 4 R-cue and 4 F-cue trials tested at each of 3 delays (0, 5, and 10 s). A single probe trial occurred randomly within each block of 5 regular trials. On probe trials, comparison stimuli were always presented regardless of the nature of the cue presented on that trial, and correct responses were reinforced with 3 s access to mixed grain. Incorrect responses on probe trials resulted in a 3-s blackout. The delay-interval duration was varied on probe trials only.

### RESULTS AND DISCUSSION

The mean percentage of correct matching responses obtained during cue-testing sessions is presented in Fig. 2. Accuracy was significantly lower on F-cue trials than on R-cue trials, $F(1,11) = 47.02$, $p<0.0001$, and it declined with increases in delay interval, $F(2,22) = 179.19$, $p<0.0001$. Accuracy was also significantly higher on short-sample trials than on long-sample trials, $F(1,11) = 7.24$, $p<0.05$. The analysis also revealed significant interactions of type of cue by sample duration, $F(1,11) = 10.87$, $p<0.01$, delay interval by sample duration, $F(2,22) = 14.38$, $p<0.001$, and type of cue by sample duration by delay interval, $F(2,22) = 4.28$, $p<0.05$. On R-cue trials, there was no significant difference in accuracy between short- and long-sample trials at any delay. However, on F-cue trials, accuracy on short-sample trials was significantly greater than on long-sample trials at the 5-s delay, $F(1,11) = 14.16$, $p<0.01$, and at the 10-s delay, $F(1,11) = 27.03$, $p<0.001$, but not at the 0-s delay ($F<1$). In addition, accuracy was significantly lower on F-cue trials than on R-cue

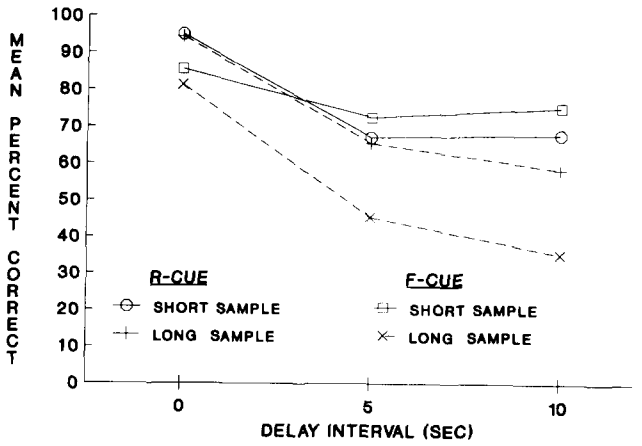


FIG. 2. Mean percent of correct matching responses as a function of type of cue (remember or forget cue) and sample duration (short or long) during testing at delays of 0, 5, and 10 s.

trials under all conditions except short-sample trials at the 5- and 10-s delay.

While a directed forgetting effect with temporal samples has been previously reported (31), in that study, accuracy on short- and long-sample trials was not reported separately, nor was the delay interval varied. Consequently, the present data are the first to show that explicit cues to forget a temporal sample accelerates the rate at which the analogical code in working memory is foreshortened. A choose-short effect is clearly evident on F-cue trials at the 5- and 10-s delays. On R-cue trials at the 10-s delay, a choose-short effect is beginning to appear, but it is not large enough to be statistically significant. Memory of the temporal sample is foreshortening on R-cue trials, but not at the rate that it is on F-cue trials.

## GENERAL DISCUSSION

The present findings are in part consistent with the previously reported disruptive effects of scopolamine on matching of nontemporal events, in that disruption occurs at even the shortest delay interval (6, 7, 11, 17–19, 21, 23, 38–40, 42, 51, 55). The lower level of accuracy produced by scopolamine at the 0- and 1-s delay may suggest that scopolamine is simply disrupting choice behavior generally. However, if it were acting in this way, there would be no reason to anticipate the emergence of a choose-short effect under scopolamine at delay intervals that do not produce such effects under saline. Given the nature of temporal coding by pigeons, there is evidence that, in addition to any general disruptive effects, scopolamine is having a specific effect on the rate at which the analogical code for time is foreshortened in working memory. According to the subjective shortening model (47), reference memory for the association between event durations and the comparison stimuli becomes established during initial training and remains stable, provided that the original delay interval remains in effect on a substantial number of trials. On trials for which the original delay interval is increased, the event duration maintained in working memory subjectively foreshortens. The discrepancy between the reference memory of the event duration and the shortened working memory of the event duration is responsible for the choose-short effect. The effect of scopolamine on this subjective shortening process appears to be very similar to that produced by presenting the pigeons with an explicit cue to forget the event duration. Although the form of scopolamine used in the present study has both central and peripheral effects, it is highly likely that the results observed were due to its central effects. Our previous work (38–40) has shown that injections of the centrally active form of scopolamine disrupted working memory in pigeons much more than equivalent injections of the peripherally active form.

Due to the relatively short delay intervals used in the present experiments, a significant choose-short bias did not appear on saline sessions or on R-cue trials. The choose-short effect is quite robust (22, 43–45, 47, 57), and undoubtedly would have been evident on saline sessions had longer delay intervals been used. It began to be evident on R-cue trials at the 10-s delay in Experiment 2. The choice of shorter delay intervals was required in order to maximize sensitivity of the design to the hypothesized effects of scopolamine and F-cues on the rate of subjective shortening.

It is difficult to compare the present effects of scopolamine on temporal discriminations in pigeons with those effects reported for d-amphetamine (46,50) and tetrahydrocannabinol (6). The effects of d-amphetamine at a 0-s delay interval have been inconsistent, because both a choose-short (50) and a choose-long bias (46) have been reported. Increased doses of tetrahydrocannabinol have been accompanied by greater choose-short biases at a 0-s delay (6). This suggests that higher doses of scopolamine might produce a choose-short bias at even a 0-s delay.

The data obtained in the present research support the hypothesis that manipulation of the neurotransmitter acetylcholine affects behavior in tasks requiring memory processes not only in mammalian species, but in an avian species as well. While previous research with a variety of species has indicated that tasks that require working memory rather than reference memory are more susceptible to the effects of anticholinergics (3, 5, 24, 35, 38–40, 56, 58), it has been difficult to isolate the specific cognitive processes affected. While many reasons could account for this, one possibility is that the categorical nature of the memory code in most delayed response tasks makes it difficult to detect these effects. The present research suggests that memory for event duration may be a particularly sensitive procedure for investigating amnesic drugs. Behavioral research has supported the hypothesis that the memory code for event durations is analogical rather than categorical (45,57), and that this analogical code is subject to foreshortening (47). The present results support the hypothesis that anticholinergic blockade accelerates the rate at which memory for temporal events is foreshortened in working memory. This effect is similar to that produced by an explicit cue to forget the sample.

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