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BRIEF COMMUNICATION

The Effect of d-Amphetamine on Short-Term Memory for Time in Pigeons

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SPETCH, M. L. AND D. TREIT. *The effect of d-amphetamine on short-term memory for time in pigeons.* PHARMACOL BIOCHEM BEHAV 21(4) 663–666, 1984.—The effect of d-amphetamine on pigeons' perception and short-term memory of time was investigated within a delayed symbolic matching to sample paradigm in which pigeons were rewarded for choosing one color after a 1-sec sample and another color after a 5-sec sample. On trials with no delay between sample offset and onset of the choice phase, d-amphetamine produced a bias toward choosing the color that was correct after long samples, suggesting that the birds overestimated the sample durations under amphetamine. With a 20-sec retention delay, d-amphetamine lowered choice accuracy to chance level, suggesting that it impaired the birds' short-term memory for sample durations. It was postulated that an amphetamine-induced increase in the rate of perceptual processing could mediate the effects of amphetamine on both time perception and memory.

d-Amphetamine Time perception Short-term memory

SEVERAL lines of evidence suggest that amphetamines can produce a systematic change in the perception of time. Studies in humans have suggested that amphetamines produce an overestimation of real time intervals (e.g., [4]). Although the results of some initial studies in animals suggested that amphetamines disrupted timing accuracy and increased baseline response biases, rather than lengthening perceived time [12,16], recent studies have produced results similar to those found in human subjects. Using a variety of procedures, several investigators have provided strong evidence that methamphetamine can produce an overestimation of real time intervals in rats [8, 9, 10, 11].

The present experiment was designed to extend this work on amphetamine and time perception by examining the effect of d-amphetamine on pigeons' short-term memory for time intervals. A version of the delayed symbolic matching to sample (DSMTS) task was used in which pigeons were trained to peck one color following a short duration sample and another color after a long duration sample (cf. [13]). The birds were tested at three retention delays (0-sec, 5-sec, and 20-sec) between the sample offset and the choice period. This task allowed an assessment of the effect of d-amphetamine on pigeons' time perception (0-sec delay performance) as well as its effect on their short-term memory of sample duration (5- and 20-sec delay performance).

METHOD

Five naive White King pigeons, maintained at 85% of their free-feeding body weights, served as the subjects. The test environments consisted of operant conditioning chambers that each contained three horizontally aligned pecking keys, a food hopper, and a house light. Projectors mounted behind each key were used to illuminate the keys with either white, red, or green fields of light. Input and output from the operant chambers were controlled by a PDP 8/e computer.

Predrug Training

During preliminary sessions, each bird was trained to eat from the food hopper and to peck at the illuminated response keys. The birds were then trained on the DSMTS procedure, in which trials began with the presentation of a trial-initiating stimulus (illumination of the center key with white light). A single peck to the trial initiating stimulus terminated it and produced the sample, which consisted of either a short (1 sec) or a long (5 sec) houselight presentation. Sample offset was followed by illumination of two pecking keys, one with red and one with green light (i.e., the comparison stimuli). A peck at one comparison stimulus was reinforced (with 4 sec of food access) only if it had been preceded by a short sample, whereas a peck at the other comparison was reinforced only if it had been preceded by a long sample. Because the particular key color that was correct after long and short samples was varied across the birds, responses to the comparison associated with the short samples will be referred to as "short" responses, and those to the comparison associ-

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TABLE 1

PERCENTAGE OF TRIALS INITIATED AND CHOICE ACCURACY AS A FUNCTION OF DOSE OF d-AMPHETAMINE FOR THE TWO PIGEONS IN THE PILOT STUDY*

Bird	Dose	% of Trials Initiated	Delay:	Percent Correct 0-sec		5-sec		20-sec	
			Sample:	Long	Short	Long	Short	Long	Short
1	4 mg/kg	26		94	67	71	43	84	29
	3 mg/kg	49		68	56	75	53	57	56
	2 mg/kg	100		87	67	76	61	53	59
	1 mg/kg	100		88	83	57	53	51	51
	0.5 mg/kg	100		92	88	67	75	46	63
	0 mg/kg	100		92	92	69	66	47	65
2	3 mg/kg	43		72	32	47	68	24	47
	2 mg/kg	71		83	71	69	69	49	71
	1 mg/kg	79		76	81	42	87	60	73
	0 mg/kg	93		86	87	70	72	50	75

*Doses were tested in a mixed order for Pilot Bird No. 1, and in an ascending order for Pilot Bird No. 2. For both birds, each drug session was alternated with at least one control (0 mg/kg) session.

ated with long samples as "long" responses. Incorrect responses resulted in termination of the trial without reinforcement. Trials were separated by a 30-sec intertrial interval (ITI), and 48 trails were scheduled in each daily session.

Following approximately 50 sessions of training under the DSMTS procedure, delays between the sample and comparison were introduced. Within each session, 0-sec delays continued to occur on a random half of the trials. On the remaining trials delays of 5 and 20 sec occurred, each with a probability of 0.5. The birds were trained under this variable delay condition for 50 additional sessions.

Drug Testing Procedure

Prior to the drug testing phase, each bird received an intraperitoneal injection (cf. [5]) of saline (0.5 ml/kg) on each of two baseline days in order to habituate them to the injection procedure. Following habituation, the birds were injected (IP) with either 2 mg/kg of d-amphetamine sulphate dissolved in saline, or with an equivalent volume of saline 10 min before each of ten test sessions. This dose was chosen because it is within the range found to affect pigeons' temporal discrimination, both in previous studies [16] and in our own pilot work (Table 1), but it is well below the range at which gross side-effects such as stereotypy typically appear [5]. For each bird, drug sessions alternated daily with saline control sessions. Three birds started the test regimen with a saline condition and two with a drug condition so that both conditions were represented on each of the 10 test days. During each session the birds' accuracy after short and long samples at each delay was recorded. In addition, the proportion of trials in each session on which a response was made to the left key was recorded. These proportions were then converted into percent deviation from chance (50%) to provide an index of position biases.

RESULTS

Figure 1 shows the five birds mean choice accuracy after short and long samples at the three delays during the saline and amphetamine conditions, averaged over the five sessions under each condition. At the 0-sec delay, there was no appreciable difference between accuracy after short and long samples under saline, whereas under d-amphetamine, accuracy was higher after long samples than after short samples. Conversely, at the 20-sec delay, accuracy was much higher after short samples than after long samples under saline, but under d-amphetamine this difference was not present. Thus, d-amphetamine appeared to produce a bias toward making "long" responses at the 0-sec delay, while eliminating a baseline bias toward making "short" responses at the 20-sec delay.

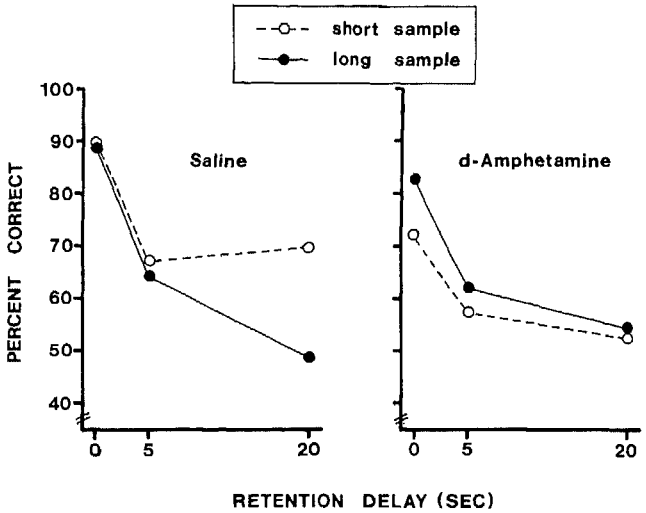

FIG. 1. Mean choice accuracy after short and long samples at the three delays under the saline control condition (left panel) and the d-amphetamine condition (right panel).

A three-way repeated measures analysis of variance of these choice data revealed a significant main effect of drug condition, $F(1,4)=419.04$, $p<0.0001$, and of delay, $F(2,8)=20.72$, $p<0.001$, but not of sample duration, $F(1,4)=1.34$, $p>0.1$. In addition, there was a significant two-way interaction between drug condition and sample duration, $F(1,4)=8.54$, $p<0.05$, and between delay and sample duration, $F(2,8)=7.21$, $p<0.05$, but not between drug condition and delay, $F(2,8)=1.54$, $p>0.05$. Finally, there was a significant three-way interaction between drug condition, delay, and sample duration, $F(2,8)=5.42$, $p<0.05$. Subsequent post-hoc comparisons (Newman-Keuls, $p=0.05$) confirmed the observations that at the 0-sec delay, accuracy after long samples was significantly greater than accuracy after short samples under d-amphetamine but not under saline. Conversely, at the 20-sec delay, there was no significant difference between accuracy after short and long samples under d-amphetamine, whereas under saline accuracy after short samples was significantly greater than accuracy after long samples. At the 5-sec delay, the differences in accuracy after short and long samples did not reach significance under either d-amphetamine or saline.

These effects of d-amphetamine did not appear to change as a function of the number of drug administrations. An analysis of variance of choice accuracy across the five days of drug administration yielded no significant main effect of days, $F(4,16)=1.05$, $p>0.1$, and no significant interaction between days and any other factor (all ps>0.1).

The effect of d-amphetamine on the magnitude of the birds' position biases was assessed by comparing the percent deviation scores under the saline and d-amphetamine conditions with a t-test for dependent measures. This analysis showed that the magnitude of position biases under saline (Mean=7.42%) was not significantly different, $t(4)=0.03$, $p>0.5$, from that under d-amphetamine (Mean=7.36%).

DISCUSSION

The effect of 2 mg/kg of d-amphetamine on pigeons' ability to discriminate sample duration in the present study is compatible with previous reports that amphetamines produce an overestimation of real time intervals in rats [8, 9, 10, 11] and in humans [4]. At the 0-sec delay, pigeons displayed a systematic bias toward making "long" responses under d-amphetamine, suggesting that they tended to overestimate the duration of short samples. Since this bias was not present under the saline condition, and since it interacted with delay, it does not appear to reflect a simple exaggeration of preexisting response tendencies (cf. [3, 12, 16]). Furthermore, d-amphetamine had no systematic effect on baseline position biases. Thus, the present results appear to provide further support for the idea that amphetamines lengthen perceived time, perhaps by accelerating the operation of an "internal clock" (cf. [4,9]).

In addition to extending the work on amphetamines and time perception, the present study examined the effect of 2 mg/kg d-amphetamine on pigeons' memory for time. At 20-sec retention delays, d-amphetamine was found to increase the relative proportion of "long" responses. One interpretation of this result is that the pigeons remembered sample durations that had been subjectively "lengthened" by d-amphetamine, and thus tended to respond "long" more often. However, certain features of the data are not in accordance with this hypothesis. First, performance at the 20-sec delay under d-amphetamine was not characterized by an absolute bias toward making "long" responses; instead, d-amphetamine diminished the baseline tendency to choose "short." Second, the birds' choice accuracy under d-amphetamine was near chance level after both short and long samples at the 20-sec delay, suggesting that sample duration was exerting little control over their responses. Perhaps the simplest interpretation of the 20-sec delay results, therefore, is that in addition to lengthening the perceived duration of the samples, d-amphetamine produced a general short-term memory deficit. Such a deficit might eliminate control by sample duration at long delays and thus override the perceptual changes produced by the drug. This interpretation is supported by recent evidence that amphetamines can disrupt short-term memory processes in animals [1,7].

It should be noted that the pattern of results obtained in the saline condition is comparable to that obtained in previous behavioral studies of animals' short-term memory for time [2, 14, 15]. Although it is typically the case that memory for colors or lines is facilitated by increasing the sample duration (e.g., [13]) better memory for the longer of two samples is not found when duration is the dimension along which the samples are discriminated [2, 14, 15]. Instead, animals show a bias toward choosing the comparison that is correct for short samples, which results in more accurate performance on short-sample trials. Since this bias only occurs at long delays, it has been interpreted in terms of guessing strategies that are used in the absence of sample information [2], or in terms of subjective shortening of the sample duration over the delay interval [15].

The generality of the present results across different doses of d-amphetamine remains to be determined. The 2 mg/kg dose used in the present study was chosen on the basis of previous research [5,16], and on the basis of our own pilot data (see Table 1). Our pilot data suggested that doses of d-amphetamine 1 mg/kg or lower did not produce robust effects in our task, while doses 3 mg/kg or higher tended to disrupt the pigeons' willingness to initiate trials. Thus, even though 2 mg/kg of d-amphetamine has reliable effects on pigeons' performance in the present task, our pilot data suggest that the range of doses at which these effects can be easily detected may be quite narrow.

It is possible that an amphetamine-induced increase in the rate of perceptual processing could underlie both the perceptual and the memorial effects hypothesized to account for the present data. First, if time perception is based upon the rate at which internal or external events are perceived (cf. [4,10]), then an amphetamine-induced acceleration of perceptual processing would cause more events to be perceived within a given time interval and make the interval seem longer. Second, if short-term retention of sample information is disrupted by subsequent extraneous stimuli [6,17], then this same amphetamine-induced increase in perceptual processing might expose the animal to more potentially interfering stimuli during the delay, and thereby lead to greater memory loss (cf. [1]). Thus, a single mechanism may account for the effects of amphetamine on both time perception and short-term memory.

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