Effects of Δ^9-tetrahydrocannabinol on delayed matching-to-sample choice speeds in chimpanzees*

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The effects of Δ^9-THC on choice response speeds in chimpanzee short-term recognition memory were assessed in a delayed matching-to-sample task. Choice speeds were faster on correct than on incorrect trials and were inversely related to delay length. Although Δ^9-THC lowered matching accuracy, it did not affect any aspect of choice speed. These results were interpreted as indicating that the disruption of short-term recognition memory produced by Δ^9-THC reflects changes in acquisition-storage processes rather than in memory retrieval processes.

The delayed matching-to-sample procedure may be operationally classified as a recognition memory task inasmuch as the S is required to identify, from among two or more alternative choices, the sample stimulus which was presented prior to an ensuing retention interval. In a recent series of chimpanzee experiments with this recognition task, we have established that Δ^9-tetrahydrocannabinol (the major active constituent of marihuana) impairs short-term memory, as reflected by decrements in the percentage of correct choice responses (Ferraro, 1972; Ferraro & Grilly, 1972, 1973; Ferraro et al, 1973; Grilly et al, 1973).

In apparent contrast to the pervasive effect obtained for Δ^9-THC on matching accuracy, we have not observed any acute drug effect on mean choice response speed, i.e., the mean speed of responding to one of the alternative choice stimuli (e.g., Ferraro & Grilly, 1973). Several other investigators have found that choice reaction time (the reciprocal of choice response speed) is a sensitive indicant of delayed matching-to-sample task parameters in human and nonhuman primates. More specifically, mean choice reaction time has been shown to increase with increasing delays and, at any given delay, to be shorter for correct than for incorrect choice responses (e.g., Jarrard & Moise, 1971).

In an attempt to pursue further the relationship between choice response speed and accuracy and to assess the effects of Δ^9-THC on this relationship, we have submitted a portion of our previously obtained choice response speed data to a more detailed distributional analysis.

METHOD

Subjects and Apparatus

The present report is based primarily on unpublished choice response speed data obtained in prior experiments, the publications of which provide detailed descriptions of the Ss, materials, and apparatus used (Ferraro & Grilly, 1973; Ferraro et al, 1973). Briefly, data are presented for five adult and eight juvenile chimpanzees who had previously had extensive training on the delayed matching-to-sample task at delay intervals ranging from 0 to 63 sec. The principal apparatus was a stimulus-response panel, which contained four response keys and a 1-g monkey-pellet dispenser. Three of the response keys were horizontally aligned and served as choice stimulus keys. The sample stimulus key was centered above the three choice keys. Each key could be separately illuminated with color and form stimuli.

Procedure

Under the delayed matching-to-sample task, a trial began with the presentation of a sample stimulus. Ten consecutive responses to the sample response key terminated the sample stimulus and initiated a fixed delay interval, during which no stimuli were presented. Following the delay, a different choice stimulus was presented on each of the three choice response keys. A response to the choice stimulus which matched the previously presented sample stimulus was reinforced, and terminated the trial. An incorrect response to either of the nonmatching choice stimuli simply terminated the trial. Successive trials were separated by an intertrial interval of 15 sec. Latencies of responding to the onsets of the choice stimuli were recorded in 10ths of seconds and then were converted to reciprocal speed scores. In order to prevent confounding from within-delay responding, latencies shorter than .5 sec, which occurred on less than 1% of the trials, were eliminated from the analyses.

Although the data to be presented for delays of 10, 20, 40, and 63 sec were taken from different experiments, certain communalities existed in the procedures. First, all chimpanzees were given at least 14 nondrug control sessions under the specified delay value. Two and one-half hours prior to each of these sessions, the chimpanzees were orally administered the drug vehicle alone. Next, 3 to 5 consecutive drug sessions were run. The drug treatment at each delay consisted of orally administering 1.0 mg/kg Δ^9-THC in the drug vehicle 2.5 h prior to the matching-to-sample session.

RESULTS

The mean choice response speed data presented for the nondrug control condition in Table 1 were as anticipated from the delayed matching-to-sample data reported by Jarrard & Moise (1971). Mean choice response speed for all trials combined decreased as the

Table 1
Delayed Matching-to-Sample Mean Choice Response Speeds Obtained Across All Trials and Separately for Correct and Incorrect Trials at Four Delay Intervals Under Nondrug Control and 1 mg/kg Δ^9-THC Drug Treatment Conditions

	Control			Δ^9-THC		
Delay (Sec)	All	Correct	Incorrect	All	Correct	Incorrect
10	.85	.85	.78	.77	.79	.68
20	.72	.74	.60	.69	.72	.60
40	.68	.70	.60	.69	.70	.57
63	.57	.59	.44	.59	.60	.52

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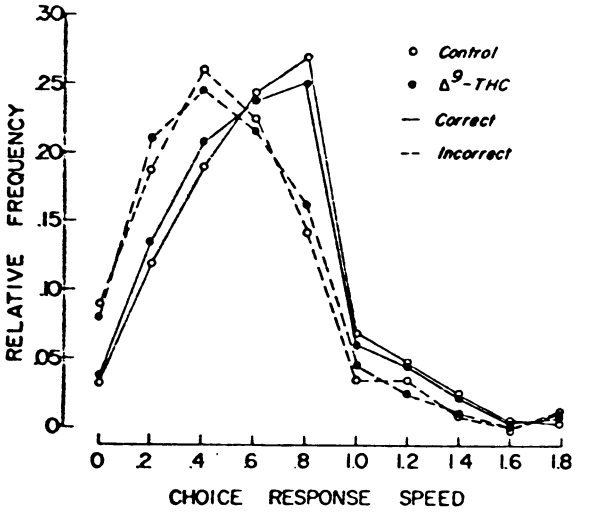

Fig. 1. Mean relative frequency distributions of choice response speeds on correct and incorrect delayed matching-to-sample trials across delay values for nondrug control and 1-mg/kg Δ^9-THC drug treatment conditions. The numbers given on the abscissa represent the lower bound of each category of choice response speed.

delay interval was increased, and correct choices were executed with faster speed than were incorrect choices. The same general relationships between choice response speed and delay and correctness of response are shown for the drug condition in Table 1. Between control and drug conditions, there was some tendency for Δ^9-THC to produce slower choice response speeds at the shorter delay values. However, separate pairwise comparisons between drug and control conditions at each delay value in no case yielded a significant drug effect on mean choice response speed.

Relative frequency distributions of choice response speeds on correct and incorrect trials were separately constructed for control and drug conditions at each delay value. The shapes of the distributions at each delay were very consistent. Consequently, these separate distributions were averaged together for presentation in Fig. 1. Succinctly stated, Fig. 1 serves to elaborate the fact that Δ^9-THC did not produce an effect on choice response speed despite the existence of clear-cut significant differences between the speed of responding on correct and incorrect trials. In this context, it should be noted that Δ^9-THC reliably produced a decrease in the percentage of correct responses. For the distributions shown in Fig. 1, the overall percentage correct matching was 82.4% under the control condition and 73.7% under the drug.

In an attempt to elucidate further the relationship between percentage correct matching and choice response speed, the previously mentioned relative frequency distributions for each delay were redistributed into different size choice response speed categories so that each chimpanzee had at least 20 trials in each category. The percentage correct matching for each choice speed category was then computed. Once again, the resulting functions were entirely consistent between delays, so the averaging across delays was justified.

Figure 2 presents mean percentage correct matching as a function of choice speed for control and drug treatment conditions. As can be seen in Fig. 2, a direct relationship pertained between matching accuracy and response speed. Separate analyses of variance performed at each of the four delays showed, in fact, that this relationship was significant in each instance for both control and drug conditions. However, a difference does emerge in Fig. 2 between control and drug conditions. Specifically, the drug data are displaced downward in matching accuracy by an approximately constant factor for each choice speed category. Thus, for any given choice speed category, matching accuracy was lower under the drug. As before, separate analyses of variance yielded significant differences in matching accuracy between control and drug treatment conditions at each matching-to-sample delay value investigated.

DISCUSSION

The present analyses of delayed matching-to-sample choice response speeds serve both to confirm previous findings and to suggest a mechanism by which Δ^9-THC may affect short-term recognition memory. In the first instance, the findings that mean choice response speed is faster at short delays and for correct responses replicate the data presented in a number of experiments (e.g., Jarrard & Moise, 1971; Milner & Ettlinger, 1972; Stone, 1969). Furthermore, the fact that quantitatively similar relationships existed under nondrug and drug conditions is consistent with our previous reports that Δ^9-THC does not affect overall choice response speed, even though it does significantly impair matching accuracy (Ferraro & Grilly, 1973; Ferraro et al, 1973).

There were several bases for expecting that Δ^9-THC should decrease choice response speed. Empirically, complex reaction

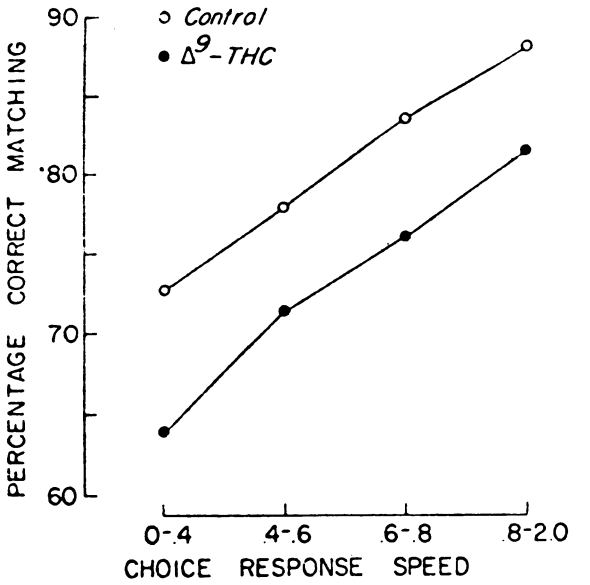

Fig. 2. Percentage correct matching averaged across all delays as a function of choice response speed for nondrug control and 1-mg/kg Δ^9-THC drug treatment conditions. Note that the separate choice response speed categories given on the abscissa are of different sizes.

time and choice latency in short-term memory experiments have been shown to increase under marihuana (Clark et al, 1970; Darley et al, 1973). Additionally, Δ^9-THC is known to increase the proportion of longer latency incorrect matching trials as compared to nondrug matching performance.

On the other hand, if choice response speed is assumed to reflect a S's retrieval criterion for acceptance of an incorrect alternative from memory, as may be inferred from some signal detection theories of short-term memory (e.g., Murdock, 1968), then choice speed would be expected to increase under Δ^9-THC. This is because Abel (1971a b), among others, has shown that marihuana produces a lowered criterion value in recognition memory tasks. The fact that choice speed was unaltered while matching accuracy was decreased by Δ^9-THC in the present experiment mitigates the likelihood of a drug-produced retrieval failure and tends, instead, to implicate an impairment of acquisition-storage processes.

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Rats barpress in order to change the rate at which they are fed*

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Four rats were fed irregularly but on the average of once every 3 min. If a rat pressed a bar, the average interfeeding interval dropped to once every 30 sec. All four rats learned to barpress. When barpresses no longer changed the average interfeeding interval, the rats tended not to press. A reintroduction of the relation between barpressing and reduction of the interfeeding interval generated renewed barpressing.

Herrnstein & Hineline (1966) and Herrnstein (1969) have argued that the principal reinforcement in avoidance learning is the reduction of the temporal frequency (rate) of aversive events. Herrnstein & Hineline (1966) arranged a situation in which rats were shocked irregularly but with a constant average rate irrespective of their behavior. If a rat barpressed, the average rate of shocks received by him would decrease for a brief period of time following the barpress until the delivery of the next shock, then the rate of shock presentations would be restored to its former level. Rats learned to barpress, and barpressing rates were shown to be dependent upon response-contingent percentage reduction in shock rate.

Fantino (1969) had argued that pigeons responding on concurrent chain schedules of positive reinforcement will prefer the key which leads to more immediate reinforcements. Herrnstein (1961, 1964) had argued that stimuli associated with greater rates of reinforcement will be better conditioned reinforcers than stimuli associated with lesser rates of reinforcement.

A general hypothesis emerges from the foregoing: animals will respond to receive a higher rate of positive reinforcers or a lower rate of aversive events, or the stimuli associated with them. In the standard operant conditioning situation, a rat receives no reinforcers when he does not press a bar, and receives a reinforcer each time he does press. This situation is merely one point on a continuum of infinitely many possible relations between rate of reinforcement (or aversive stimulation) prior to instrumental behavior and rate of reinforcement (or aversive stimulation) following a response. Such an instrumental conditioning space has been proposed by Seligman, Maier, & Solomon (1971) and Catania (1971).

In the traditional view, temporal contiguity between a

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