

*SHORT-TERM MEMORY IN THE RHESUS MONKEY:
A BEHAVIORAL ANALYSIS OF
DELAYED-RESPONSE PERFORMANCE*

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This study obtained quantitative data on the bodily orientations of rhesus monkeys in a delayed-response task and determined whether such orientations mediate the correct response in a choice trial. The basic task was a two-key chain schedule with the key leading to food signaled in the initial component. During the subsequent delay interval, the signal was removed, but it was necessary that one of the keys be pressed to advance the schedule to the terminal choice component. The position of the key pressed thus indicated orientation during the delay interval. When the monkeys had free access to the left and right keys, they tended to press the key leading to food throughout the chain schedule components and received food on more than 85% of the trials, even when the delay was extended to 20 seconds. However, when orientation toward the food key was disrupted by forcing the monkeys to press an extraneous center key during the delay, choice performance deteriorated. Requiring the center key presses early, rather than late, in the delay component had a strong disruptive effect. The relation of the results to the mediating coding-response hypothesis is discussed.

Key words: short-term memory, delayed response, delayed conditional discrimination, retroactive interference, coding response, mediation, key press, monkeys

Recent research on human short-term memory has stimulated interest in short-term memory of nonhuman animals (D'Amato, 1973; Jarrard, 1971; Medin & Davis, 1974; Medin, Roberts, & Davis, 1976; Shimp, 1976). One of the important questions about short-term memory in both man and lower animals is how a stimulus controls responding when a period of time intervenes between the presentation of the stimulus and the opportunity to emit the response. A delayed-response task has been used to address this question with animals. The task is a conditional-position discrimination with a delay interval between the presentation of a cue signaling the correct position and the opportunity to choose between two positions. Since Hunter's (1913) observation of correlations between delayed-

response performance and bodily orientations to goal objects, it has been suggested that bodily orientations can be used to retain the correct position during the delay interval (e.g., French, 1959), although there is also evidence against this notion (e.g., MacCorquodale, 1947; Tinklepaugh, 1928). Except for a few studies (e.g., Gleitman, Wilson, Herman, & Rescorla, 1963), however, the descriptions of bodily orientations have been anecdotal and unquantified, and no attempts have been made to examine whether observed bodily orientations actually are used to retain the correct position during the delay interval.

The purpose of the present experiment was to obtain precise and quantitative information on bodily orientations of rhesus monkeys during performance of a delayed-response task and to examine the influence of bodily orientations on the level of performance. In order to measure bodily orientations quantitatively, a new delayed-response procedure was devised. When the delayed-response task is studied, using the Wisconsin-General-Test Apparatus for example, the animal responds to one of two identical objects that cover the foodwells. The correct position is marked by baiting one of the foodwells in the animal's sight. After the delay interval the animal can reach the objects

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to get the food. In the present study two keys were used instead of objects covering food-wells. The task was a chain schedule with the correct position (key) signaled in the initial component by a colored light behind one of the keys. During the subsequent delay interval, the positive stimulus was removed, but it was necessary that one of the keys be pressed to advance the schedule to the terminal component. The position of the key pressed thus indicated the orientation of the monkey during the delay interval. In the terminal component of the chain, both keys were illuminated with the positive stimulus; reinforcement required that the monkey respond on the same key that was associated with the stimulus during the initial component. After key press orientation was determined by this procedure, the opportunity to press the correct key during the delay interval was removed. In this condition it was necessary that a third extraneous key be pressed during the delay interval to advance the schedule. Thus, data were obtained concerning whether interference with the monkey's orientation to the correct key during the delay interval would disrupt delayed-response performance.

METHOD

Subjects

The subjects were three male rhesus monkeys (Monkeys 429, 491, and 498) weighing 5.9, 7.1, and 4.8 kg, respectively. They were maintained at about 90% of these free-feeding weights throughout the experiment.

Apparatus

The monkeys were trained in a chamber, measuring 50 cm by 54 cm (floor dimensions) by 60 cm (wall height). One wall contained a panel with four translucent plastic keys, 4

cm in diameter, arranged in a diamond. The two horizontally located keys and the upper key were used. The two horizontal keys were spaced 26 cm apart and were 35 cm above the floor. The upper key was located 43 cm above the floor. A minimum force of .05 N was required to operate a microswitch behind each key. Three colored lamps (24 VDC) were located behind each key to project red, green, or white lights on the keys. Two 30-W fluorescent lamps illuminated the experimental room, and masking noise was continually present. A pellet dispenser delivered a soybean. The operant chamber was interfaced to a Digital Equipment Corporation PDP-8f computer, which arranged contingencies, presented stimuli, and recorded data.

Procedure

Preliminary training. The monkeys first were trained to press each of the keys when it was illuminated. The position and the color of the illuminated key varied over trials. Initially, each key press was reinforced by a soybean. Then a 10-sec fixed-interval schedule of reinforcement was introduced. Preliminary training was continued for 20 sessions, by which time the monkeys showed stable responding without long pauses. During subsequent conditions the monkeys were trained on the tasks described below and summarized in Table 1.

Delayed-Response I. The three monkeys were trained on a delayed-response task involving only the horizontal keys (Delayed-Response I). Each trial had three components, cue presentation (C), delay (D), and choice response (RESP), as shown in the left of Figure 1. The three components were signaled by different stimuli, and the monkeys were required to press a key at least once to advance from one component to another (a chain schedule). Following the intertrial interval when

Table 1
The Number of Sessions during the Main Part of the Experiment

Monkey	DR I	DR I	DR I	DR II	DR I	DR II	DR III
		1st reversal	2nd reversal		with longer delays	with longer delays	
429	23	21	21	19	25	25	10
491	18	6	13	15	25	25	10
498	25	29	—	12	25	25	10

DR I: Delayed-Response I; DR II: Delayed-Response II; DR III: Delayed-Response III.

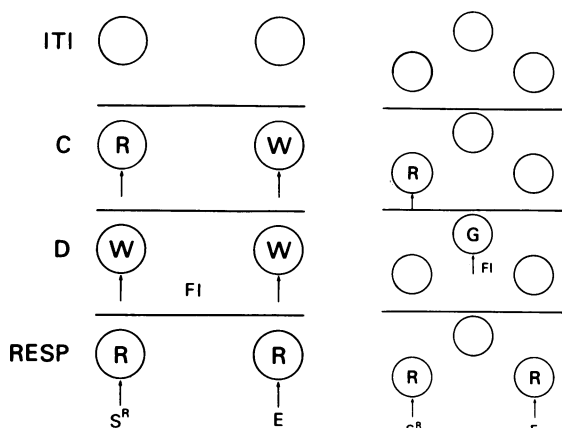


Fig. 1. *Left:* A diagram illustrating the Delayed-Response I procedure. Circles indicate the left and right keys, and arrows indicate key presses. The abbreviations ITI, C, D, and RESP refer to intertrial interval, cue, delay, and response components respectively. The letters R and W in the circles indicate the color of the keys, that is, red and white. The reinforcement schedule of the cue and the response components was a fixed ratio of 1 and that of the delay component was a fixed interval (FI) of 4 sec. A left trial is illustrated. Thus, a response on the left key was reinforced by a soybean (S^R) and a response on the right key was an error (E). *Right:* A diagram illustrating the Delayed-Response II procedure. The color of the upper key during the delay component was green (G). Other details were the same as those of the Delayed-Response I procedure.

the keys were dark (the top left row of Figure 1), the two keys were illuminated during the cue component (the second row). The color of one key was red, and the other was white, with the position-color combination randomly varied from trial to trial. A single press on either key changed the colors of the keys so that both keys were illuminated with white lights, marking the beginning of the delay component (the third row). A single press on either the left or the right key occurring after the 4-sec delay interval changed the colors of both keys from white to red. During the response component (the fourth row), a single response on the key that had been red in the cue presentation component was reinforced by a soybean. A response on the key that had been white in the cue component constituted an error. Both correct and incorrect responses turned off the red lamps and terminated the trial. Correct and incorrect responses were followed by intertrial intervals of 10- and 30-sec respectively. The key that was pressed in each component was recorded: that is, the key press in the cue component, the last press in the

delay component, and the key press in the choice-response component. The number of key presses during the delay was also recorded. Fifty trials were given in daily sessions. Training was continued until the monkeys reached a performance criterion of 90% or more correct responses in three successive sessions.

Delayed-Response I: Reversals. The color of the keys in the delay component was green rather than white in this condition. After six sessions with red as the positive stimulus, the reversal condition was introduced. On the first reversal the three monkeys were reinforced for pressing the key that had been white during the cue component. Otherwise, the procedures were the same as before. When 90% or more correct responses occurred for three successive sessions on the first reversal, a second reversal was conducted with two monkey (429 and 491). The contingencies of the second reversal were the same as those of Delayed-Response I, except that the color of the keys was green during the delay component. As before, correct responses were followed by a 10-sec intertrial interval. Errors were followed by a longer intertrial interval, usually 30 sec, but as long as 120 sec when the monkeys showed strong position preferences. When a 120-sec intertrial interval was employed, the number of trials in a session was reduced to 20. Lengthened intertrial intervals were introduced between Sessions 6 and 16 for Monkey 429, between Sessions 6 and 25 for Monkey 498 in the first reversal, and between Sessions 6 and 14 for Monkey 429 in the second reversal. Training on the second reversal was continued until 90% or more correct responses occurred in three successive sessions.

Delayed-Response II. In Delayed-Response I the monkeys could press the correct key throughout the delay component. However, in Delayed-Response II, which utilized the upper key as well as the two horizontal keys, the monkeys were required to press the upper key in the delay component, as shown in the right-hand part of Figure 1, thus preventing orientation toward the correct key. In the initial cue component, either the left or the right key was illuminated red (Monkeys 429 and 491) or white (Monkey 498) according to a random schedule. The other keys were dark. A single response to the illuminated key terminated the keylight and the upper key was illuminated green, marking the beginning of

the delay component. A single response to the upper key after 4 sec terminated the green keylight, and both left and right keys were illuminated red. During the response component a single response to the key that had been illuminated in the cue component was the correct response and was reinforced by a soybean. A response to the opposite key, that is, the one not illuminated during the cue component, was scored as an error. All other features of the training were the same as in Delayed-Response I.

Delayed-Response I and II with longer delays. After the acquisition criterion was reached with the Delayed-Response II procedure, Monkeys 429 and 491 were retrained with the Delayed-Response I procedure, and Monkey 498 was retrained on the reversal condition of Delayed-Response I. Then, using the procedures, five delay intervals were studied: 4, 8, 12, 16, and 20 sec. The delay interval always was the same in each daily session of 50 trials, and each delay interval was studied for a total of 5 sessions (a total of 250 trials for each delay). The order of sessions devoted to the different delay intervals was random. The monkeys next were trained on Delayed-Response II again. After the acquisition criterion was attained, the five delay intervals again were studied. Throughout, correct responses were followed by the 10-sec intertrial interval, and errors were followed by the 30-sec intertrial interval.

Delayed-Response III. In a third variant of the delayed-response task (Delayed-Response III), the effects of the interpolation of upper-key presses during the delay were studied further. Before the introduction of this task, Monkeys 429 and 491 were retrained with Delayed-Response I, and Monkey 498 was retrained on the reversal condition of Delayed-Response I. The procedure of Delayed-Response III is illustrated in Figure 2. In the cue component (the top row in Figure 2), either the left or the right key was illuminated red, and the other key was colored white. The position of the red and white lights was changed randomly. A single response to either the left or the right key advanced the chain from the cue component to the delay component. In this task the delay component was divided into two periods (the second and third rows) each involving a fixed-interval schedule (chain FI FI). The monkeys had to press

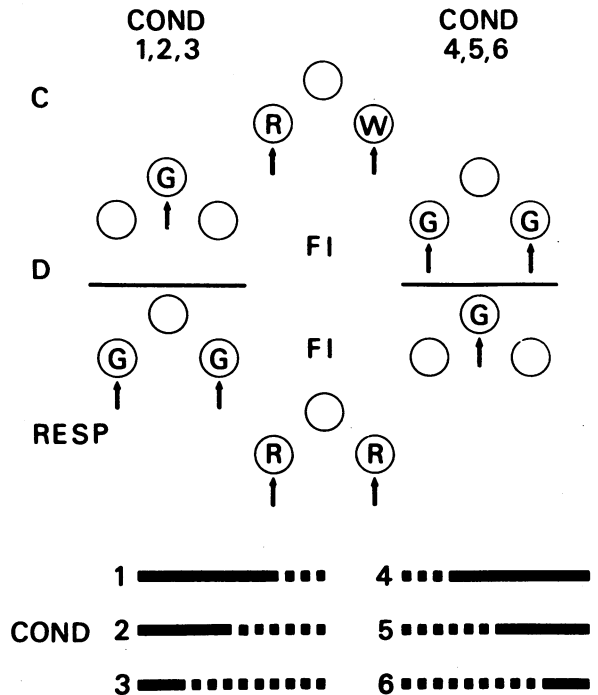


Fig. 2. *Upper:* A diagram illustrating the Delayed-Response III procedure. A single key press on either the left or the right key, colored red (R) or white (W), advanced the trial from the cue (C) to the delay (D) component. The color of keys was green during the delay component, which was divided into two parts; that is, a chain FI FI schedule was in effect. Presses on the upper key were required in the first part of the delay component in Conditions 1, 2, and 3, and were required in the latter part of the delay component in Conditions 4, 5, and 6. Throughout, the other part of the delay component was similar to that of earlier procedures, in which a press on either of the horizontal keys, both colored green, advanced the schedule. *Lower:* A diagram of the time allotted to the two parts of the delay component in each condition of Delayed-Response III. The part of the delay in which upper-key presses were required (black bars) was 9 sec for Conditions 1 and 4, 6 sec for Conditions 2 and 5, and 3 sec for Conditions 3 and 6. The part of the delay in which upper-key presses were not required (dotted lines) was 3 sec for Conditions 1 and 4, 6 sec for Conditions 2 and 5, and 9 sec for Conditions 3 and 6.

the upper key (disruptive key presses) in one of these periods, as in Delayed-Response II. In the other period the monkeys could press the left or the right keys, as in Delayed-Response I. The duration of each period was 3, 6, or 9 sec, and the sum of the two fixed-interval periods was always 12 sec. As summarized in Figure 2, there were six conditions. For Conditions 1, 2, and 3, the monkeys were required to press the upper key in the first period. For

Conditions 4, 5, and 6, disruptive upper-key presses were interpolated in the second period. In the choice response component (the fourth row), the color of both keys became red. For two monkeys (429 and 491), the correct response was a press on the key that had been red in the cue component. For Monkey 498, however, a response to the key that had been white in the cue component was correct, and a response to the other key was an error. The 10-sec intertrial interval followed a correct response, and an error was followed by the 30-sec intertrial interval. All 6 conditions were presented during each session. There were 60 trials with each condition occurring 10 times in a random sequence. The monkeys were tested for 10 sessions. Usually the monkeys were tested 7 days a week, and each session

was terminated by either the number of trials described above or by a time limit (1 hr).

RESULTS

Delayed-Response I

The number of sessions required to attain the criterion (including the three criterion sessions) was 17, 12, and 19 for Monkeys 429, 491, and 498, respectively. Each monkey showed position preferences before the delayed-response task was mastered.

Position of key presses. Figure 3 shows the patterning of effective key presses during the acquisition phase of the Delayed-Response I procedure. Effective presses were those that advanced the schedule components; that is, the first (and only) presses in the cue and

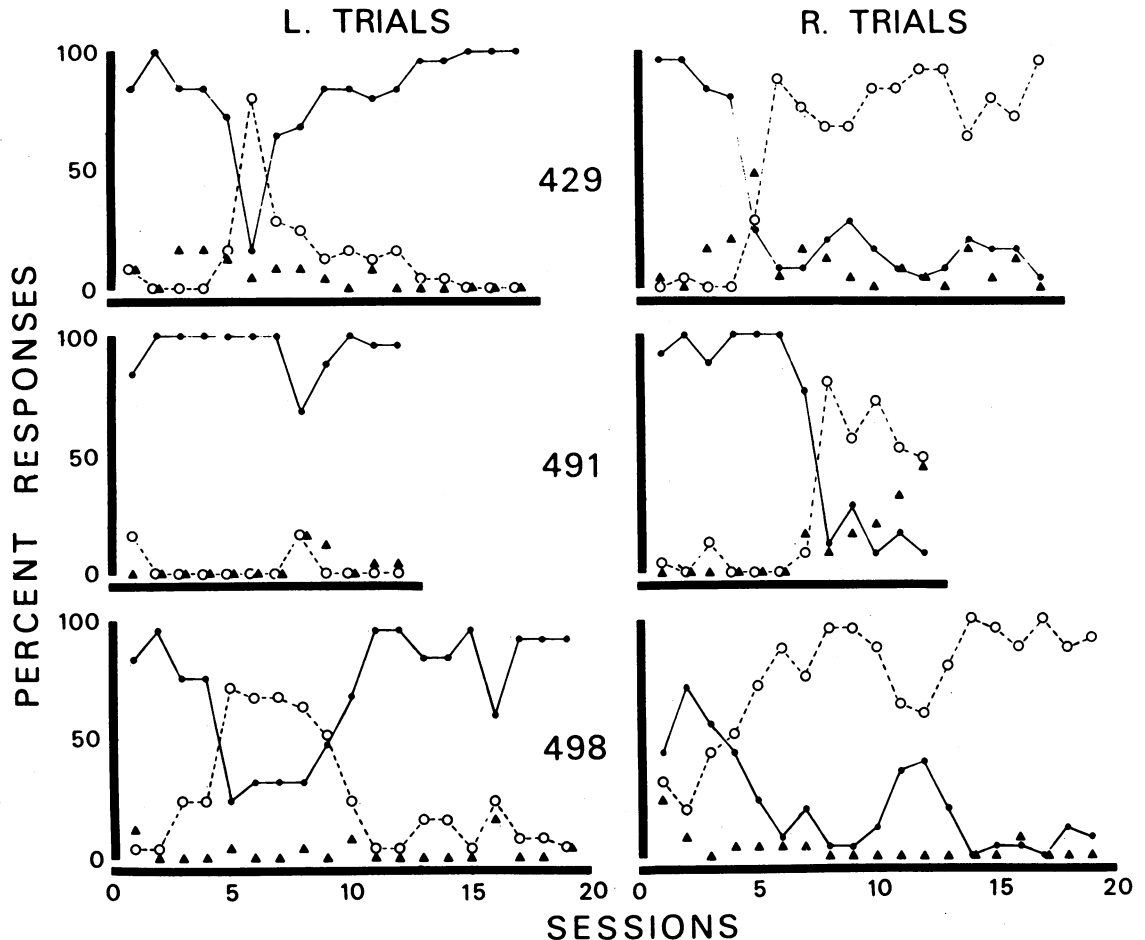


Fig. 3. Patterns of the three effective key presses during the acquisition phase of Delayed-Response I. The percentages of trials in which all three responses were on the left key or on the right key are shown by filled and unfilled circles. Triangles indicate the percentage of trials with other key-press patterns. The left and right panels show trials in which left and right key presses were reinforced in the response component.

Table 2

The number of presses on the left and the right keys during the delay component of the three criterion sessions.

Cue Position	Final Choice	(Result)	Monkey 429			Monkey 491			Monkey 498		
			No. of Trials	Left key presses	Right key presses	No. of trials	Left key presses	Right key presses	No. of trials	Left key presses	Right key presses
Left	Left	(Correct)	75	369	0	73	401	1	70	478	0
	Right	(Error)	0	—	—	2	3	4	5	0	34
Right	Left	(Error)	9	47	0	8	38	0	5	28	0
	Right	(Correct)	66	0	304	67	8	255	70	0	480

choice response components and the last press in the delay component. The percentages of trials in which all three presses were on the left key or on the right key are shown by filled and open circles respectively. Triangles indicate the percentage of trials with other patterns. During the delay component the monkeys emitted 1.20 (Monkey 429), 1.18 (Monkey 491), and 1.70 (Monkey 498) presses per sec. Table 2 shows the number of presses during the delay component that were made on the left and the right keys during the three criterion sessions. Together, Figure 3 and Table 2 indicate that the monkeys generally pressed the same key throughout a trial. Before the discrimination was acquired, the preferred key was chosen throughout. However, after the task was learned the monkeys began pressing the red key in the cue component and continued pressing on that key for the remainder of the successful trials. In 27 of the 29 error trials that occurred during the criterion sessions, the monkey began pressing the white key in the cue component and continued to do so for the remainder of the trial.

Reversals

The number of sessions taken to reach the criterion for the first reversal was 21, 6, and 29 for Monkeys 429, 491, and 498 respectively. Monkeys 429 and 491 reached the criterion of the second reversal within 21 and 13 sessions respectively. Discriminative control under the previous contingencies disappeared within the first session of the reversals. During the early sessions of reversal training, strong position preferences appeared, as illustrated for Monkey 429 in Figure 4. In the first reversal the subject responded to one key throughout virtually all trials until correct performance emerged after about 15 sessions. At the end of

training, the white key was chosen during the cue component, and that orientation was maintained throughout a trial. A similar pattern appeared in the second reversal. Analysis of errors during the criterion sessions of both reversals indicated that in virtually every case an incorrect choice occurred at the beginning of these trials and was maintained throughout the trials, as during earlier sessions that were characterized by position preferences.

Delayed-Response I and Delayed-Response II with Longer Delays

The number of sessions to reach criterion during initial training with the three-key Delayed-Response II procedure was 19, 15, and 12 for Monkeys 429, 491, and 498 respectively.

Figure 5 shows performances under the Delayed-Response I and Delayed-Response II conditions at delay intervals ranging from 4 to 20 sec. Each subject showed a high percentage of correct trials under Delayed-Response I, even when the delay interval was extended to 20 sec. However, two monkeys (491 and 498) did not maintain a high performance level in Delayed-Response II when the delay interval was lengthened. This demonstrates the deleterious effects of responding on the upper key during the delay component. The third monkey (429) showed efficient levels of performance with both procedures. Direct observation using a television monitor revealed that this monkey, unlike the others, directed his head to the correct side during the delay interval.

Delayed-Response III

Figure 6 shows the effects of requiring upper-key presses during a part of the delay component, together with the results of the

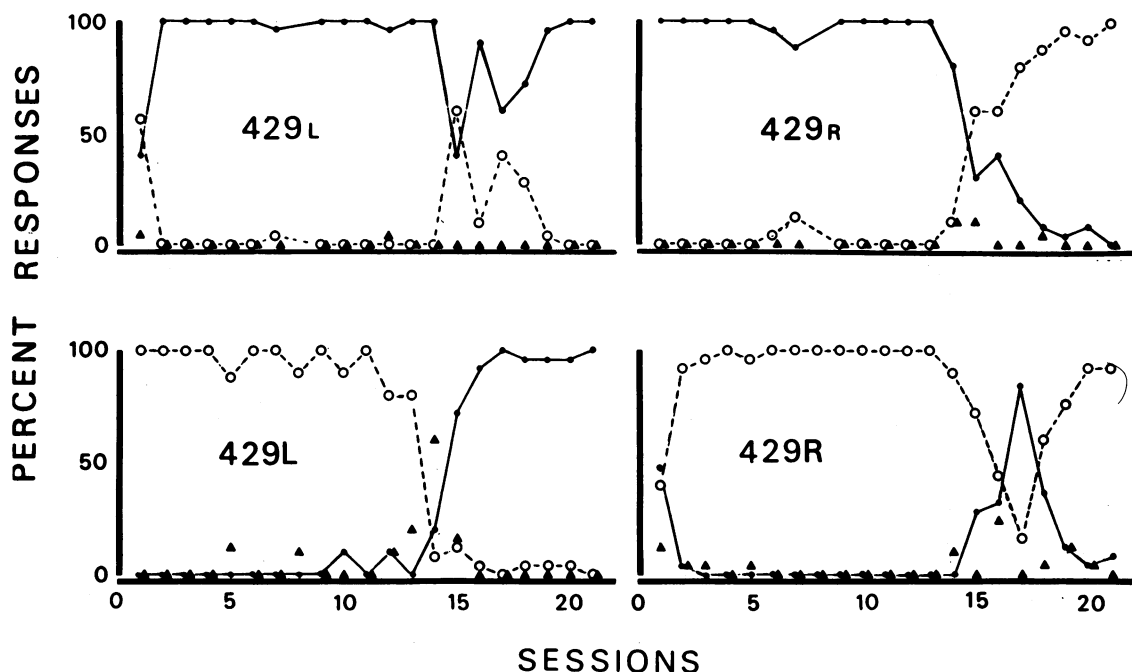


Fig. 4. Patterns of the three effective key presses of Monkey 429 during the first (upper figures) and the second (lower figures) reversals of Delayed-Response I. The letters L and R indicate left and right trials. Other details are the same as those in Figure 3. Data from Session 8 in the first reversal was lost.

Delayed-Response I and II procedures with 12-sec delay interval. Although there was considerable session-to-session variation in percent correct responses, each monkey showed better performance in Conditions 4, 5, and 6 than in Conditions 1, 2, and 3. In Conditions 4, 5, and 6, the monkeys showed 84% to 91% correct responses, the same level of performance occurring with the Delayed-Response I procedure. In Conditions 1, 2, and 3, however, the performance of the monkeys deteriorated to 61% to 81% correct responses, the same level of performance occurring with the Delayed-Response II procedure for two of the three monkeys (491 and 498). As described before, Monkey 429 oriented his head toward the correct key in the Delayed-Response II procedure. This bodily orientation was not maintained in the Delayed-Response III task; thus, requiring upper-key presses during the early part of the delay reduced the likelihood of a correct choice in the response component for all three monkeys. Figure 6 also shows that the duration of the period of disruptive key presses did not affect the accuracy of choices, which was the same whether the period of upper key presses lasted 3, 6, or 9 sec.

DISCUSSION

The coding-response hypothesis, which was proposed and elaborated with reference to matching-to-sample and delayed matching-to-sample tasks, states that each sample stimulus occasions the emission of sample-specific response chains (coding-responses) which mediate performance (Blough, 1959; Cumming, Berryman, & Cohen, 1965; Eckerman, 1970; Lydersen & Perkins, 1974; Shimp & Moffitt, 1977). The results of the present experiment suggest that the coding-response hypothesis may apply to delayed-response performance. When monkeys had free access to left and right keys during a delay (Delayed-Response I), the delayed-response task was performed efficiently, even when the delay interval was lengthened to 20 sec. Analyses of behavior within successful trials indicated that after the monkeys mastered the task, the correct key was pressed throughout the cue-, delay-, and choice-response components of the trials. Thus, on left trials the monkeys pressed the left key, and on right trials they pressed the right key throughout the trial components. In contrast, when the monkeys were required to press an

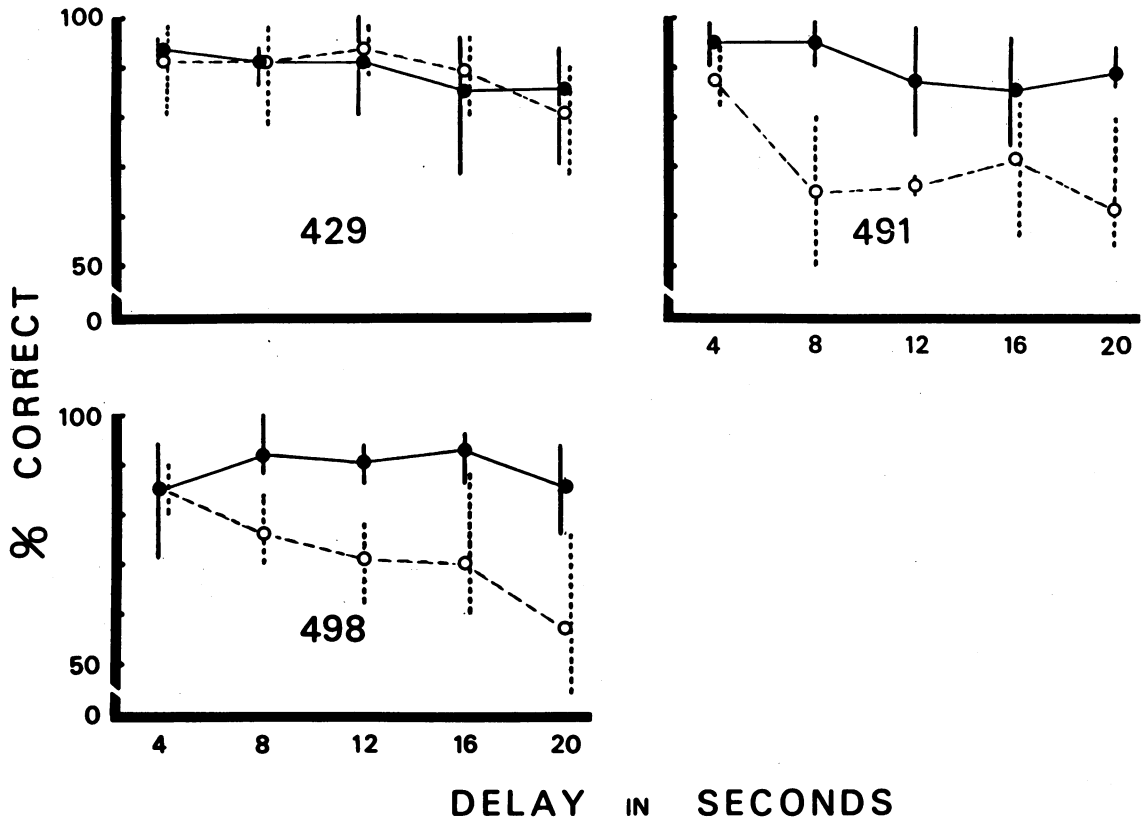


Fig. 5. Mean percent correct trials in each delay interval for Delayed-Response I (filled circle) and Delayed-Response II (open circle) in each monkey. Each bar indicates the range across sessions.

additional key and thus were prevented from pressing the correct key during the delay (Delayed-Response II), the performances of two of the three monkeys fell to chance levels when long delays were employed. Together, these results suggest that differential key-press orientations during the delay interval mediated choice of the correct key-press position in the choice-response component. The decrement in performance in Delayed-Response II may indicate a limited capacity of the monkeys for short-term memory without mediating response chains (coding responses).

The interpolation of disruptive key presses had different effects in the present study as compared to results of studies using delayed matching-to-sample tasks. These other studies (Etkin, 1972; Maki, Moe, & Bierley, 1977; Moise, 1970; Roberts & Grant, 1978) found the duration of interpolation of disruptive events to be important. In one study (Roberts & Grant, 1978), a disruptive event had a stronger effect when it was interpolated in the later

part of a delay interval. However, in the present study the duration of the disruptive event had no differential effect on performance in a delayed-response task. Instead, the important factor for performance was *when* the disruptive events occurred. Only when the disruptive event was interpolated at the beginning of the delay did it have a strong negative effect on performance. The difference between delayed response and delayed matching-to-sample may stem from a difference in the dimension of the cue. That is, the dimension of the cue was spatial in the present delayed-response procedure, but is nonspatial in delayed matching-to-sample procedures. Monkeys may acquire mediating response chains more easily when the cue is spatial than when it is the color or pattern of visual stimuli. Because of a possible lack of mediating response chains during the delay, animals may be more susceptible to proactive inhibitory effects in delayed matching-to-sample tasks than in delayed-response tasks (Grant, 1975; Herman, 1975; Jarrard & Moise,

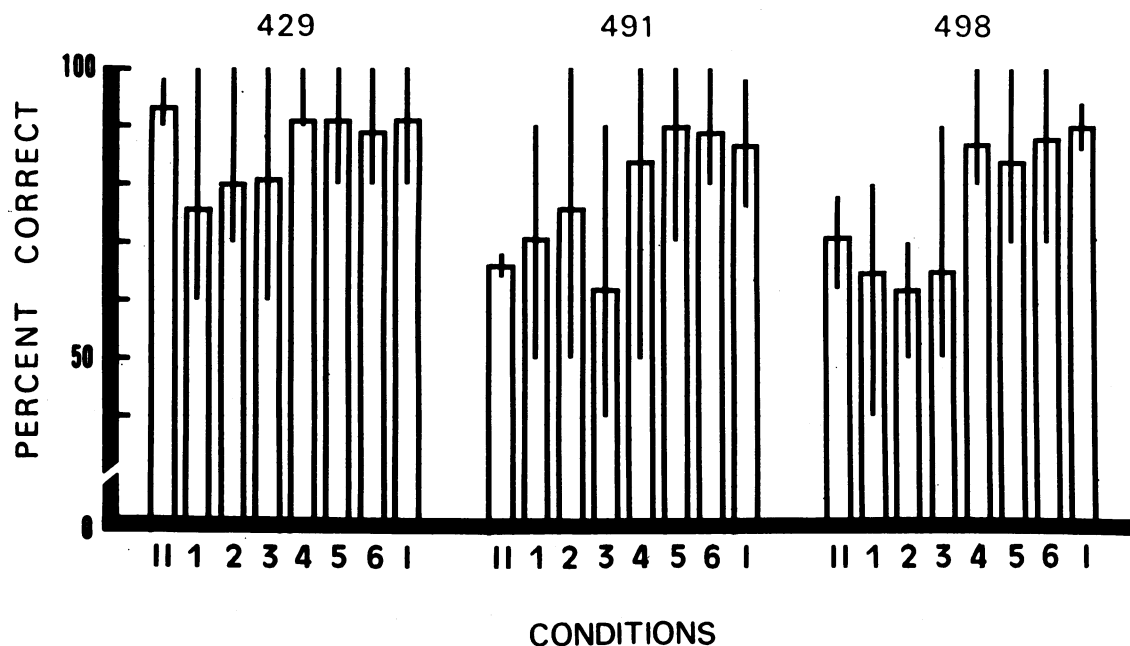


Fig. 6. Mean percent correct responses in each condition of Delayed-Response III, along with the data of Delayed-Response I (I) and Delayed-Response II (II) at 12-sec delay interval. Each bar inside the columns indicates the range across sessions. Note that performance was always lower when upper-key presses were required in the first part of the delay component, that is, in Conditions 1, 2, and 3.

1971; Maki et al., 1977; Mishkin & Delacour, 1975; Moise, 1976; Nelson & Wasserman, 1978; Worsham, 1975). One study that supports the present results concerning effects of interpolating disruptive key presses was concerned with the effects of electrical stimulation of the monkey's prefrontal cortex during different periods of a delayed-response trial (Stamm, 1969). Performance fell to chance levels only when the stimulation occurred during the late cue and early delay periods of the task, a finding roughly parallel to the present data.

Borkhuis, Davis, and Medin (1971) studied delayed-response performance using a 4×4 matrix stimulus display. In the cue component 2 of the 16 cells were illuminated with different colors. The correct position was white, and the other was red. A response on the cell that had been red in the cue component was designated as a confusion error. Borkhuis et al. described two possible sources of confusion errors. One source of error is that subjects discriminate stimuli properly, but the distinctive features of the stimuli become obscure during the delay. The other possibility is that perceptual confusion occurs at the time of encoding, that is, in the cue component. An

analysis of error probabilities led the authors to conclude that confusion errors reflect the latter possibility. The results of the present experiment indicated that when the monkeys acquired the delayed response, most errors occurred as a result of incorrect choices in the cue component. This finding thus supports Borkhuis and her co-workers' theoretical analysis, and, along with the result of the interpolation of disruptive key-presses, it suggests that the initiation of an appropriate response chain at the beginning of a trial plays an important role in delayed-response performance.

Finally, it should be noted that an alternative interpretation of the present findings can be expressed without recourse to hypothetical memorial processes. On a given trial of Delayed-Response I, several response patterns could eventuate in reinforcement (e.g., if the cue was initially on the left, the sequences LLL, LRL, RLL, or RRL all were reinforced). Thus, the response chains that developed may have reflected acquisition of a stereotyped pattern that satisfied the reinforcement contingency with the least effort (cf. Vogel & Annau, 1973). The present experiment was not designed to test these two possible interpreta-

tions. In the Delayed-Response I procedure, however, different response chains were developed between left and right trials. Thus, it may be possible that these stereotyped response patterns had a mediating function.

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