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ANALYSIS OF THE EFFECTS OF FRONTAL LESIONS IN MONKEY: II. VARIATIONS OF DELAYED RESPONSE[1]

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The initial study of this series (5) tested the hypothesis that frontal operates fail both delayed alternation and delayed response because they have difficulty with the left-right response choice which these tasks require. Specifically, after the delay period of either task, the monkey is confronted with two containers which are distinguishable only by their positions—one cup appears on the left, the other on the right. In delayed alternation, for example, the correct mode of response is simply to alternate between the two cups; yet the performance of frontal operates rarely rises above chance. In the earlier study, therefore, frontal operates' performance on traditional left-right alternation was compared with their performance on two variants of alternation. In one variant, monkeys were trained to displace, alternately, two cups arranged one above the other—an up-down alternation; in the other, they were trained to alternate between displacing and not displacing a single centered cup (i.e., displace the cup on one trial, leave it alone on the next, displace it on the third trial, and so on)—a "go–no-go" alternation. Results on the up-down problem, which showed that frontal operates perform this task as poorly as they perform the traditional left-right alternation, disproved the original hypothesis.

On the "go–no-go" problem, however, the same operates achieved a performance level of nearly 90 per cent correct. The first of the present experiments was undertaken to determine whether similar improvement would result in frontal operates' *delayed-response* performance, if delayed response were varied from the traditional "left-right" task to a "go–no-go" task. Positive results would permit an analysis, using additional delayed-response variations, aimed at isolating the factors responsible for the frontal operates' improved performance. The second experiment proceeds with this analysis.

METHOD

Subjects

Eight immature macaques were used throughout this study: Four (LF 2, 3, 5, and 11) had bilateral anterolateral frontal ablations, and four (TF 4, 15, 26, and 37) had bilateral inferotemporal ablations. All but one (TF 37) had served as *S*s in the earlier experiment (5). The data for the present experiment were gathered in the interval four months to nine months after operation. Anatomical data on the four frontal and four temporal control operates may be found in references 5 and 9, respectively.

Apparatus

The apparatus consisted of an enclosure divided into two sections—an unlit chamber for the animal cage and an illuminated section for the testing tray, to which either one or two cups were attached. A sliding plywood panel was lowered between the two sections to hide the cups from the animal during the delay period. A one-way vision screen concealed *E* when the sliding panel was raised.

EXPERIMENT I

All animals were trained on classical delayed response and on the variation. Each task was presented by both the direct method of cueing, in which the animal is shown the correct cup being baited with food, and by the indirect method, in which the animal is shown an object signaling the baited cup.

Procedure

Traditional, direct method. For the traditional procedure the sliding panel was raised, a peanut was held for an instant over the left or the right cup (these were 12 in. apart and beyond the animal's reach), the peanut was dropped into it, and the cup covered with a lid. The panel was lowered for 5 sec., the tray pushed forward, and the panel raised again to permit the animal to respond. If the animal displaced the lid of the baited cup, it obtained the reward.

Variation, direct method. The variation on delayed response, analogous to the variation on delayed alterna-

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tion used in the previous study, was presented in the following way: The sliding panel was raised, a peanut was held for an instant over a *single centered cup* (placed beyond the animal's reach), dropped into the cup, and covered with the lid. The panel was lowered for 5 sec., the cup pushed forward, and the panel was raised to permit response. This was a "go" trial; i.e., if the animal displaced the lid it found the reward. On a "no-go" trial, the panel was raised, *E* displayed an empty hand, and closed the lid of the empty cup. The panel was lowered for 5-sec. delay, the tray was pushed forward, and the panel was raised again. If it displaced the lid *on this trial*, *S* found the cup was empty. This "no-go" trial was scored correct only if the animal did not manipulate the lid in the 5 sec. permitted for response.

The "go" and "no-go" trials were presented in a predetermined, balanced order, as were the "left" and "right" trials in the traditional procedure. Fifty trials a day, with delayed self-correction for errors, were presented for 500 trials on each task, unless the animal attained the criterion of 90 correct in 100 trials before this training limit was reached. Two animals from each operate group received the traditional procedure first, and two received the variation first. In both tests the intratrial delays were 5 sec., with the panel interposed, and 5 sec. was permitted for response.

After completing these two tasks, all animals were given further training on the variation presented by the direct method with longer intratrial delays. Each animal received 30 trials a day (with delayed self-correction for errors) for three days. Within each daily session an equal number of 5-, 10-, and 15-sec. delays were presented in a predetermined, balanced order; at each delay, half the presentations were "go" trials and half were "no-go" trials.

Traditional, indirect method. For traditional delayed response presented by the indirect method, the stimulus object employed for half the animals was a round gray ash tray and for the other half, a square, colored tobacco tin. In the predelay period, the object appeared on top of one of the two covered cups, indicating which one contained the reward.

Variation, indirect method. For the variant procedure both objects were used with each animal. When one object (the same as that used in the traditional procedure) appeared on top of the single centered cup, it indicated that the cup *did* contain food and that the correct response was "go"; the other object indicated that the cup did *not* contain food, and that the correct response was "no go."[3]

In both tests, the object was always removed during the 5-sec. delay period. The two tests were again balanced for order, and in all other respects the training procedures were identical to those used with the direct method of baiting.

Results

The results, shown in Table 1, are the same for both the direct and indirect methods of baiting. On traditional delayed response, all control operates attained the 90 per cent criterion in less than 250 trials; all frontal operates received 500 trials and still performed at a chance level. On the variation procedures, however, all operates, frontals as well as controls, achieved criterion in less than 250 trials. The controls averaged somewhat fewer trials than the frontals on the delayed response variations, but there was considerable overlap between the learning scores of the two groups.

TABLE 1

Results, Experiment I

(Scores are number of trials, including criterion run, required to attain the criterion of 90 per cent correct in 100 consecutive trials. A score of 500 trials denotes failure to reach criterion, and is accompanied by the per cent correct achieved in the final 100 trials on that task.)

Subjects	Traditional		Cue and Response Variation	
	Direct	Indirect	Direct	Indirect
LF 2	500 (53)	500 (58)	120	100
LF 3	500 (56)	500 (63)	160	140
LF 5	500 (56)	500 (53)	250	210
LF 11	500 (49)	500 (58)	210	250
TT 4	100	100	140	100
TT 15	160	100	110	110
TT 26	250	180	130	100
TT 37	100	100	160	160

The average percentage correct for the three delay periods on the variation presented by the direct method (in the order 5, 10, and 15 sec.) were as follows: Temporal operates—92, 92, and 88; frontal operates—90, 81, and 79. The frontal animals thus showed a somewhat greater decrease in accuracy with increasing delays, yet they continued to perform well above chance at the longest delay interval. It is of interest to note that on the variation, 95 per cent of the total errors of *both* groups were made on "no-go" trials.

EXPERIMENT II

The delayed-response variation which the frontal operates learned differed in two major respects from classical delayed response, which they failed to learn. Not only was the response choice varied from the traditional "go left–go right" to "go–no go," but the predelay cues

[3] All the animals had been trained previously in "go–no-go" *visual discrimination* (9) using the same two discriminanda.

TABLE 2
Cue-Response Variations for Experiments I and II

Cue	Response	
	Where (2 cups)	Whether (1 cup)
Where (1 cue)	Classical	Response varied
Which (2 cues)	Cue varied	Cue and response varied

were varied from the traditional "bait left–bait right" to "bait–no bait." The differences may be paraphrased this way: Instead of choosing *where* to go on the basis of *where* the cue had been presented, the animal must now choose *whether* to go on the basis of *which* cue had been presented. The following experiment was designed to answer which of these two variations, the change in the cue or the change in response choice, was more effective in eliciting successful performance by the anterofrontal operates.

Table 2 presents a two-by-two classification, indicating the cue-response combinations which define classical (upper left) and variant (lower right) delayed response as used in the first experiment, together with the two new variations presented in the present experiment. Specifically, the traditional cueing by "bait left–bait right" was combined with the variant response choice, "go–no go" (upper right in the table); also the variant cueing by "bait–no bait" was combined with the traditional response choice, "go left–go right (lower left). As before, the tasks were presented first by the direct method of baiting and then by the indirect method.

Procedure

Response varied, direct method. A peanut was held about 10 in. to the left *or* to the right of a single, centered, closed cup. For half the animals (two from each group) bait on the left indicated that, following delay, the correct response was "go", whereas bait on the right indicated that, following delay, the correct response was "no go" (i.e., the single cup was empty). The other animals were trained with these cue-response relationships reversed.

Cue varied, direct method. A peanut *or* an empty hand was displayed between two closed cups. For half the animals, bait indicated that, after delay, the correct response was "go left," whereas an empty hand indicated that the correct response was "go right." The other animals were trained with these relationships reversed.

Response varied, indirect method. The stimulus object, either a tobacco tin or an ash tray, was the same as that used in the first experiment. The object (tobacco tin for four animals, and ash tray for the four others) was placed approximately 10 in. to the left *or* to the right of a singel, centered, closed cup. For half the animals, an object on the left indicated that, following delay, the correct response was "go," whereas the same object on the right indicated that, following delay, the correct response was "no go." For the other animals these cue-response relationships were reversed.

Cue varied, indirect method. This task was presented first by the following method: The tobacco tin *or* ash tray was placed in a central position, halfway between two closed cups; for half the animals the tobacco tin indicated that, after delay, the correct response was "go left," whereas the ash tray indicated that, after delay, the correct response was "go right." The other animals were trained with these relationships reversed. None of the animals showed any indication of learning this task after 200 trials, and it was apparent from observing their behavior that they were not reacting to the centrally placed stimulus. The procedure was therefore modified after 200 trials (these 200 trials were not included in the final scores) by placing the tobacco tin or the ash tray *on* the left cup for four animals and *on* the right for the other four. For the animals that were presented with the stimuli on the left cup, the ash tray indicated that the correct response was "go left," whereas the tobacco tin indicated that the correct response was "go right." For the animals that were presented with the objects on the right cup, the tobacco tin indicated that the correct response was "go right," whereas the ash tray indicated that the correct response was "go left."

The two problems presented by the direct method were balanced for order, as were the two problems presented by the indirect method, and in all other respects the training methods were identical to those used in the first experiment.

Results

The animals' learning scores and final performance on each task are shown in Table 3. In general, this series of four problems was more difficult than were the problems presented in the first experiment. Indeed, on the response-varied task with indirect baiting, no control or frontal operate attained criterion within the limits of training. However, on the response-varied task with direct baiting, three temporal operates eventually achieved 90 per cent (and the fourth, 83 per cent) correct performance, whereas none of the frontal operates met this criterion. The scores of the frontal animals *are* nearly comparable to those of the controls for those tasks in which only the cue was varied. With indirect baiting, three of the four frontal animals learned the cue-varied delayed response, and in approximately the same number

TABLE 3

Results, Experiment II

(Scores are number of trials, including criterion run, required to attain the criterion of 90 per cent correct in 100 consecutive trials. A score of 500 trials denotes failure to reach the criterion, and is accompanied by the per cent correct achieved in the final 100 trials on that task.)

Subjects	Response Varied		Cue Varied	
	Direct	Indirect	Direct	Indirect
LF 2	500 (75)	500 (65)	250	330
LF 3	500 (52)	500 (48)	500 (74)	450
LF 5	500 (50)	500 (53)	500 (74)	500 (49)
LF 11	500 (53)	500 (50)	250	100
IT 4	450	500 (54)	140	130
IT 15	500 (83)	500 (48)	290	100
IT 26	420	500 (54)	500 (75)	470
IT 37	430	500 (50)	500 (72)	210

of trials as the four controls. With direct baiting, the frontal operates again performed at approximately the same level as controls, though only two animals from each group attained the 90 per cent criterion, the others achieving a performance level of approximately 75 per cent correct.

DISCUSSION

The surprisingly small number of trials taken by frontal operates to reach criterion performance on the cue-and-response variation of *delayed response*, supports the finding of successful performance on a variation of *delayed alternation* used in the earlier study (5). This striking achievement of frontal operates in a delay situation differs from that obtained with experimental manipulations which have been attempted in the past, in that criterion performance was quickly established in all operates. Elimination of interference factors during delay (4), use of predelay reinforcement (1), and injection of barbiturates (6, 8) have not consistently improved performance to a control level; and in most instances, the improvement that did occur appeared only after lengthy training. In the cue-and-response-varied problem described in the present study, all frontal operates attained a level of 90 per cent correct in less than 250 trials, and they continued to perform well above chance with relatively long intratrial delays.

Results of the subsequent experimental analysis of this task suggest that the rapid learning by the frontal animals was due largely to the change from a positional to a nonpositional cue. That is, the frontals performed nearly as well as controls whenever a single cue presented in one of two places was replaced by one of two cues presented in a single place. This analysis of the frontal operates' performance is not conclusive, however, because of the difficulty of the tasks in Experiment 2 and because of the extensive training provided previously on similar tasks. Nevertheless, the results suggest that varying the predelay cue is relatively more effective than varying the response choice for eliciting correct delayed response in frontal operates.

These findings are important in connection with various hypotheses advanced to account for the impairment produced by anterofrontal lesions. For example, this impairment has been characterized recently as a "loss of act inhibition" (10). The facility with which frontal operates learned to avoid the food-cup completely in certain of the "go–no-go" procedures seems to contradict this hypothesis. Explanations relating specifically to frontal operates' performance on delayed response have ascribed the deficit to failure in one-trial learning, i.e., failure when competing response tendencies are established on successive trials (3, 7), to increased retroactive inhibition (4), or simply to a "defect of recent memory" (2). Yet, the present results indicate that frontal animals perform successfully tasks which are indistinguishable from the traditional tasks in terms of the conditionality and delay features on which the conceptions of impairment in one-trial learning and recent memory are based.

The present studies were not undertaken as a specific test of any of these hypotheses, and the evidence of successful performance on a variant of delayed response does not refute them. However, the fact that frontal operates show little or no impairment in the performance of a delayed-response task when it is altered simply by varying the predelay cues suggests that the (predelay) stimulus parameter is as important as are the parameters of conditionality and of delay for an adequate conceptualization of the impaired behavior resulting from frontal lesions.