NLP-18

Reprinted from The Journal of Comparative and Physiological Psychology
Vol. 51, No. 3, June, 1958 *Printed in U.S.A.*

EFFECTS OF DELAYING REWARD ON VISUAL-DISCRIMINATION PERFORMANCE IN MONKEYS WITH FRONTAL LESIONS[1]

MORTIMER MISHKIN
National Institute of Mental Health

AND LAWRENCE WEISKRANTZ
Cambridge University

An intratrial delay is the most obvious item which is common to tests that have revealed an impairment in monkeys with frontal lesions as compared with operated controls. Such tests include double alternation (4), object alternation (10), and rate-of-response alternation,[2] in addition to classical delayed response and single alternation. The cues in these tests vary widely, from auditory (1) and visual cues in delayed-response problems to response-produced cues in most of the alternation problems; and each of these cues may be subdivided further into positional and nonpositional cues. The responses likewise vary greatly, involving choices between positions, objects, or rates of response. The rewards may vary also, from the commonly used food reward to the avoidance of pain-shock (5). An intratrial delay, on the other hand, is common to all the tests, separating in each case the cue from the response and the reward.

If the failure of frontal animals on these widely varying delayed-response–type tests is due, in part, to an impairment in bridging an intratrial delay, then frontal operates should show impairment also on delayed-reward–type tests, i.e., tests in which a delay separates the cue and the response from the reward. The present experiment was designed to test this prediction. Positive results would provide a new line of evidence pointing to a relationship between the delay factor and behavioral deficit in frontal animals, and would suggest that tests involving the two types of intratrial delay measure a common neuropsychological function.

Learning with delayed reward is extremely difficult even for unoperated animals (11 ... the present study animals were trained firs... a discrimination task with immediate rew... until they met the learning criterion. ... delay of reward was introduced after learni... and the measure obtained was the effect ... this delay on the frontal animals' contin... performance on the discrimination. Unope... ated monkeys and monkeys with inferi... temporal-lobe lesions were used as controls.

METHOD

Subjects

The *Ss* were ten immature rhesus monkeys. Group A consisted of four experimentally naive, unoperated *S*s. During the course of the study two of these *Ss* receiv... anterior frontal lesions (F-168,-171), and two receiv... inferior temporal lesions (T-164,-178). Group B co... sisted of six *Ss* that had served previously in anoth... study which employed the same apparatus as that used in the present study; the *Ss* had not been train... previously on the same discriminations, however, n... on any procedure involving delayed reward. In th... earlier study, and approximately nine months befor... the present experiments were begun, anterior fronta... lesions had been made in two *Ss* (F-156,-198), a... inferior temporal lesions had been made in two *S*... (T-153,-192). The two remaining *Ss* in Group B were unoperated (N-151,-195).

Operations

The surgical procedure and the locus and extent of the two types of lesion studied in this experiment have been described in detail elsewhere (6, 9). Briefly, animals were anesthetized with Nembutal, and aseptic operat... ing techniques were used. All lesions were one-stage bilateral resections of neocortex. For the frontal lesions an attempt was made to ablate the entire dorsolateral convexity (including the banks of the sulcus principalis from the frontal pole to the level of the arcuate sulcus. In the case of the temporal lesions the attempt was to remove the ventrolateral convexity, including the middle, inferior, and fusiform temporal gyri, but sparing the temporal pole; posteriorly, these lesions extended approximately to the anterior tip of the inferior occipital sulcus. Reconstructions of the lesions will be published in a subsequent report.

[1] This study was supported in part by a grant to K. H. Pribram, Institute of Living, Hartford, Conn., from the Department of the Army, Contract DA-49-007-MD-401.

[2] Unpublished study by K. H. Pribram.

Apparatus

The apparatus consisted of a wire-mesh cage, 20 in. by 20 in. by 20 in., which contained a small panel mounted above the center of the side opposite the cage door. Pressing the panel a distance of 2 mm. closed a microswitch which could be made to activate an Anger pellet dispenser, thereby delivering a food pellet into a dish below the panel. The pellets were made of Lab Chow and pulverized peanut (P. J. Noyes Co., Lancaster, N.H.).

Four lamps were located as follows: a 40-w. white lamp on top of the cage, a 7-w. white lamp above the food dish, a 25-w. blue lamp centered on the left side of the cage, and a 25-w. red lamp either centered on the right side of the cage (in position for the "color" discrimination, described below) or mounted next to the blue lamp (in position for the "flicker" discrimination). The testing apparatus was in a soundproofed room, and the electrical programming and recording apparatus were in an adjacent room.

In addition to this testing device, which was used to study discrimination performance with delayed reward, a Wisconsin General Test Apparatus was used in the final phase of the experiment to study the performance of the animals on single alternation.

General Procedures

The experimental plan is outlined in Table 1. The general procedure, which was the same for all three delayed-reward experiments, may be illustrated by the training given Group A on the "color" discrimination. The animal was first trained to press the panel for intermittent food reward. Daily sessions were then run in which every 20 sec. the overhead light went off and the red lamp on the right *or* the blue lamp on the left came on. The colored light remained *on for* 5 sec. unless *S* turned it off sooner by pressing the panel. The *S* was trained to press while the red light was on. If *S* did press, the red light was turned off and a food pellet was delivered; if *S* failed to turn off the red light, letting it go off automatically *after* the 5 sec., then the red light was repeated on the next run 15 sec. later, and on succeeding runs, until *S* did turn it off and received the reward. Conversely, *S* was trained *not to* press when the blue light was *on*. If *S* did press, thereby turning off the blue light, then it was repeated on succeeding runs until *S* let it go off automatically (after the full 5 sec.), at which time *S* received the reward. The delivery of food was accompanied by the lighting of the food-dish lamp, which remained on for 2.5 sec. The overhead lamp was illuminated when no other lamp (i.e., red, blue, or food-dish lamp) was lit.

Twenty red-light and 20 blue-light trials, excluding rerun-after errors, were presented daily in a balanced sequence (the sequence was varied daily) until *S* reached 90 per cent correct out of the 40 trials on two successive days. After meeting the criterion, *S* was trained on the discrimination with this modification: the food reward and the food-dish light were delayed up to 8 sec. *after S* turned off the red light or let the blue light go off automatically. Errors were again followed by rerun trials, and, as before, the overhead lamp was illuminated for the entire period between stimulus presentations except when the delayed food-dish light was presented.

TABLE 1

Experimental Plan: Delay of Reward

	I	II	III
	Gradual Increase	Abrupt Increase	Gradual Decrease
	0", 1", 2", 4", 6", 8"	0", 8"	6", 4", 2", 1", 0"
Group A 2 Frontals 2 Temporals	Color (Pre and Post-op)	Flicker (Post-op)	Flicker (Post-op)
Group B 2 Frontals 2 Temporals 2 Nonoperates	Flicker (Post-op)	Color (Post-op)	

EXPERIMENT I: GRADUAL INCREASE IN DELAY

Procedure

The four *Ss* in Group A were trained to discriminate the red light from the blue light without any delay of reward in the manner described above. While, for simplicity, this is referred to as the "color" discrimination, it will be noted that the cues for the discrimination include the *position* of the lights in addition to their color. After *S* met the discrimination criterion, the reward was delayed first by 1 sec., then 2, 4, 6, and, finally, 8 sec. At each of the five delay-steps *S* was required to meet the criterion of 90 per cent correct on each of two successive days before proceeding to the next longer delay. After reaching the criterion at the longest delay, two *Ss* received bilateral frontal lesions, and two *Ss* received bilateral temporal lesions. Following a ten-day recovery period all four *Ss* were retrained by the same procedures as those used preoperatively. At the conclusion of this postoperative training schedule all *four Ss* were tested for ten additional days at the longest (8-sec.) delay.

The six *Ss* in Group B were trained in Experiment I to discriminate between an alternating light and a steady light. In this test both colored lamps were located on the left side of the cage. The stimulus which *S* was trained to turn off was a 4/sec alternation between the red light and the blue light. The stimulus which *S* was trained not to turn off consisted of both the red light and the blue light remaining on continuously. Thus, the color and position cues of the red-light-blue-light discrimination were replaced in this discrimination by flicker and brightness cues. (The alternating lights provided approximately half as much illumination as the steady lights.) For convenience the problem is referred to as the "flicker" discrimination. In all other respects, from discrimination learning through performance with the gradually increasing delays of reward, the training conditions were the same as those described for the color discrimination. Since four of the six *Ss* in Group B had already sustained cortical lesions and the two other *Ss* were serving as their nonoperate controls, Group B was tested on the postoperative phase only, receiving the gradually increasing delays only once, followed by the ten-day run at the longest delay.

Results

Having achieved criterion on the discrimination with immediate reward (the average for initial learning by all *Ss* in both training groups was 11 days, with a range of 7 to 19 days), all *Ss* needed additional training in order to achieve the criterion when the reward was delayed. Since there were no significant differences among the scores for the five delay intervals, the numbers of days required to reach the criterion at all delays, excluding criterional days, were summed to obtain a single "1- to 8-sec." score for each *S*. This extra training averaged 25 days, with a range of 9 to 58 days, though the *Ss* in Group A relearned much more quickly than this in their rerun after operation. Once the final postoperative criterion was reached, however, *Ss* had little difficulty in *maintaining* criterional performance on the longest delay.

No significant differences appeared among the operate groups on the learning, retention, or sustained performance of the delayed-reward problems. In Group A the frontal animals showed a savings of between 80 and 90 per cent, a savings equivalent to that shown by the temporal animals in reattaining criterional performance when the reward was delayed. In Group B the frontal *Ss* equaled their controls in the rate at which they learned the delayed-reward task. Finally, frontal animals in both groups continued to perform at about the 90 per cent level on the final ten-day run at 8-sec. delay (see Table 2), again matching the scores of both operate and nonoperate controls.

TABLE 2
8-Sec. Delay of Reward
Scores Are Average Per Cent Correct Achieved
Successive Days

	Experiment I Gradual Increase In Delay	Experiment II Abrupt Increase In Delay
	Group A	
F-168	92.0	59.0
F-171	92.0	59.5
T-164	96.0	75.5
T-178	95.0	77.0
	Group B	
F-156	91.5	50.0
F-198	88.0	71.0
T-153	95.5	75.0
T-192	86.0	80.0
N-151	94.5	75.0
N-195	85.5	70.0

EXPERIMENT II: ABRUPT INCREASE IN DELAY

Procedure

The negative findings in Experiment I may have been related to the technique of increasing the delay interval only gradually. Thus, delaying the reward, even by 8 sec., may have failed to disrupt, or extinguish, the frontal *Ss'* discrimination performance because they had been brought to the final criterion by a series of approximations and had been highly overtrained on the discrimination at the shorter delays. To test th[is] possibility, all *Ss* were trained on a new discrimination and after meeting the criterion were shifted abruptly to an 8-sec. delay of reward.

For this experiment the four *Ss* in Group A were transferred to the flicker discrimination while the six *Ss* in Group B were transferred to the color discrimination (see Table 1). As in the first experiment *Ss* were trained on their respective discriminations with immediate reward to the criterion of 90 per cent correct on two successive days. On the day after meeting criterion, however, all *Ss* were shifted abruptly to an 8-sec. delay of reward. The *Ss* were tested on this condition for 25 days, a period equal to the ave[rage] number of days *Ss* had received at all delay intervals (excluding criterional days) in the postoperative phase of Experiment I.

Results

The *Ss* learned their second discrimination task under the conditions of immediate reward in an average of 10 days, with a range of 3 to 19 days. There were no significant differences among the operate groups.

After they were shifted to delayed reward, however, differences among the operate groups appeared. The measure used for comparison was the average score obtained by each *S* on the last 10 days of the 25-day run. Since there was no significant change in the *Ss'* average scores between Days 16 and 20 and Days 21 and 25 (the means equaled 6[…] and 70 per cent, respectively), the scores for

...st 10 days represent relatively stable performance. As shown in Table 2, the 10-day averages varied between 50 and 80 per cent. There is no overlap between this range and the range of 86 to 96 per cent for the equivalent 10 days on the 8-sec. delay in Experiment I. Whereas all Ss thus performed more poorly in the second experiment, the frontal animals performed most poorly. The difference between the four operated Ss in Group A and the four operated Ss in Group B was not significant. The scores of these two groups were ...ed in evaluating the differences among frontal, temporal, and control groups. The average score for the frontal animals was 60 per cent as compared with 72.5 and 77 per cent for the normal animals and temporal animals, respectively. These differences were evaluated by means of Dunnett's *t* test (3) for multiple comparisons, using his table for ...ailed tests. The difference between the frontal animals and the unoperated controls was significant beyond the .05 level; the difference between the frontal and temporal animals was significant beyond the .01 level.

EXPERIMENT III: GRADUAL DECREASE IN DELAY

Procedure

A third experiment was performed to determine whether the deficit which appeared in the frontal animals when the Ss were shifted abruptly to an 8-sec. delay of reward would disappear if the delay were shortened.

Only the four Ss in Group A were studied, and they were continued on the flicker discrimination. After they had completed the 25-day run in Experiment II on the 8-sec. delay of reward, the delay was decreased to 6 ..., then 4, 2, 1, and, finally, 0 sec. The Ss were tested 10 days at each of the four delay-intervals and for ... days at the 0-sec. interval.

Results

The scores are plotted as 10-day averages in Figure 1. Included for comparison are the scores from Experiment II for the last ten days on 8-sec. delay. All Ss continued to perform at a relatively stable level from the 8-sec. through the 4-sec. delay, after which their performance began to rise. The differences between the frontal and the temporal animals ... maintained throughout all delay intervals. It is of interest that even when there ... no delay of reward—i.e., on the first ten ... of the return to the original discrimination task—the frontal Ss were still performing more poorly than were the temporal animals. Only in the second ten-day period without delay of reward do the curves for the two groups meet.

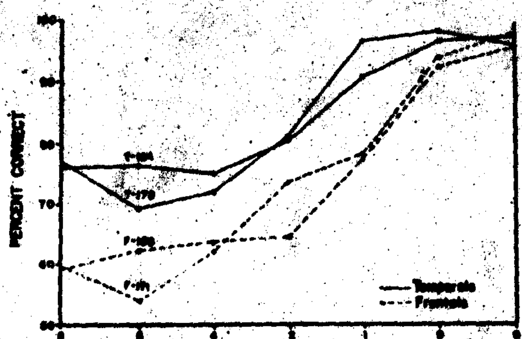

FIG. 1. Performance of *Ss* in Group A in Experiment III, gradual decrease in delay of reward.

DELAYED ALTERNATION

Procedure

After completing the delayed-reward experiments, the ten *Ss* were trained on single alternation in a Wisconsin General Test Apparatus. The *S*'s task was to displace alternately the lids of two cups mounted 18 in. apart on the testing tray. The first trial each day was an unscored free trial in which both cups were baited with peanut reward. For the first scored trial the bait was left in the cup not chosen on the free trial. After a correct choice the alternate cup was baited. After an error the concealed food was left in place until on a subsequent trial *S* chose correctly (all such rerun trials were scored). Thus, *S* was trained to alternate between the cups whether or not its previous response was rewarded. The delay between the end of the response on one trial and the opportunity for response on the next was approximately 5 sec. The cups were baited during this interval while they were screened from *S*'s view.

The *Ss* were given 30 trials a day (including reruns after errors) until they met the criterion of 90 correct in 100 consecutive trials, or, if they failed to meet the criterion, for a maximum of 1,000 trials.

Results

No frontal animal reached the criterion within the limits of training. By the end of 1,000 trials three frontal *Ss* were scoring approximately 70 per cent correct, while the fourth (F-198) remained at the 50 per cent level. All temporal and unoperated controls, on the other hand, attained the criterional score of 90 per cent correct within 600 trials, the temporal controls requiring an average of about 300 trials and the nonoperate controls slightly over 400 trials.

DISCUSSION

The results of the experiments suggest that the deficit observed in frontal monkeys on delayed-response-type tests is not a function of the position of the delay. Under certain training conditions an intratrial delay in either position—between cue and response or between response and reward—may present difficulties for frontal animals.

That it is only *intratrial* delays which present difficulties for frontal animals seems clear from other data. In the usual visual-discrimination task in which there are no delays within trials (as, for example, was the case with the discriminations presented in the initial stages of the present study), there are, nevertheless, delays of 5 to 10 sec. or more regularly intervening *between* trials. Apparently, monkeys with frontal lesions can bridge these delays successfully since generally they learn such discriminations as rapidly as do unoperated controls. Differences between frontal animals' performance on tests containing the two kinds of delay become even more apparent when frontal animals are compared with temporal controls. Thus, frontal animals are superior to temporal animals on certain tasks, e.g., difficult visual discriminations (9), in which the only delays are those occurring between trials. Conversely, frontal animals are inferior to temporal animals on other tasks, e.g., spatial and nonspatial alternations (10), in which the only regularly occurring delays are those within trials.

Considered in these terms, the evidence suggests that different neural mechanisms may be involved in bridging intertrial and intratrial delays, and that a mechanism which may serve to bridge intratrial delays is particularly susceptible to impairment by frontal-lobe damage. This interpretation of the impairment is essentially a restatement of Jacobsen's original hypothesis that monkeys with frontal lesions have a deficit in "immediate memory" (3). The restatement differs from the classical hypothesis in that, while its implications are more limited, it summarizes the more general finding of impairment on both delayed-response *and* delayed-reward tasks.

A difficulty for the present hypo[illegible] that an impairment in frontal anin[illegible] tests containing intratrial delays can [illegible] tained only under certain conditions. [illegible] present study frontal animals sho[illegible] deficit in performance under condition[illegible] 8-sec. delay of reward when the delay [illegible] creased to this interval gradually. [illegible] the technique of gradually increa[illegible] delay interval has not eliminated de[illegible] delayed-response tests, a variety of other [illegible] cedures have done so, e.g., giving pre[illegible] reward, minimizing distractions, presen[illegible] delayed-response as a "go–no go" test [illegible]. It is clear that an intratrial delay is n[illegible] *sufficient* condition for demonstrating im[illegible] ment in monkeys with frontal lesions; [illegible] nondelay variables play an important r[illegible]. This fact alone is not inconsistent with [illegible] present hypothesis which requires only [illegible] an intratrial delay constitute a *necessary* co[illegible] dition for the impairment; specifically, [illegible] impairment that is more marked in front[illegible] animals than in animals with other cort[illegible] lesions. While the results which have been re[illegible] ported in the literature appear to fulfill th[illegible] requirement, the evidence that there are im[illegible] portant nondelay features in both delaye[illegible] reward and delayed-response tests raises th[illegible] possibility that these features, rather than th[illegible] delay, are responsible for the deficit. Th[illegible] identification and isolation of the importa[illegible] nondelay conditions in delay-type tests be[illegible] comes an increasingly pressing problem i[illegible] the interpretation of the effects of fronta[illegible] lesions in monkeys.

SUMMARY

When confronted abruptly with an 8-se[illegible] delay of reward in a visual-discriminatio[illegible] task they had learned previously for imme[illegible] diate reward, frontal animals showed a sig[illegible] nificantly greater disruption or extinction o[illegible] discrimination performance than did their [illegible] operate and nonoperate controls. The data were consistent for two groups of animals trained on two different sets of discriminanda. The deficit appeared to persist throughout the series of tests given to one training group during which the delay was gradually decreased; the decrement in performance disappeared only after the delay was eliminated

[illegible] frontal animals also showed impairment [illegible] the classical single-alternation test.

While these results provide new evidence [illegible] a relationship between intratrial delays [illegible] behavioral deficit in frontal animals, and [illegible] help to define the behavioral function [illegible]h is impaired by frontal-lobe damage in [illegible]keys, other data from this study and from [illegible]vious studies indicate that caution must be [illegible]sed in interpreting the positive results.

REFERENCES

Blum, R. A. Effects of subtotal lesions of frontal granular cortex on delayed reaction in monkeys. A. M. A. Arch. Neurol. Psychiat., 1952, 67, 375-[illegible].

Dunnett, C. W. A multiple comparison procedure for comparing several treatments with a control. J. Amer. Statis. Ass., 1955, 50, 1096-1121.

Jacobsen, C. F. Functions of the frontal association area in primates. Arch. Neurol. Psychiat., Chicago, 1935, 33, 558-569.

Leary, R. W., Harlow, H. F., Settlage, P. H., & Greenwood, D. D. Performance on double alternation problems by normal and brain-injured monkeys. J. comp. physiol. Psychol., 1952, 45, 576-584.

5. Miles, J. E., & Rosvold, H. E. The effect of prefrontal lobotomy in rhesus monkeys on delayed-response performance motivated by pain-shock. J. comp. physiol. Psychol., 1956, 49, 286-292.

6. Mishkin, M., & Pribram, K. H. Analysis of the effects of frontal lesions in monkey: I. Variations of delayed alternation. J. comp. physiol. Psychol., 1955, 48, 492-495.

7. Mishkin, M., & Pribram, K. H. Analysis of the effects of frontal lesions in monkey: II. Variations of delayed response. J. comp. physiol. Psychol., 1956, 49, 36-40.

8. Morgan, C. T. The psychophysiology of learning. In S. S. Stevens (Ed.), Handbook of experimental psychology. New York: Wiley, 1951. Pp. 758-788.

9. Pribram, K. H., & Mishkin, M. Simultaneous and successive visual discrimination by monkeys with inferotemporal lesions. J. comp. physiol. Psychol., [illegible], 48, 198-202.

10. Pribram, K. H., & Mishkin, M. Analysis of the effects of frontal lesions in monkey: III. Object alternation. J. comp. physiol. Psychol., 1956, 49, 41-45.

11. Riesen, A. H. Delayed reward in discrimination learning by chimpanzees. Comp. Psychol. Monogr., 1940, 15, No. 5 (Whole No. 77).

Received April 1, 1957.