Journal of Comparative and Physiological Psychology
1963, Vol. 56, No. 1, 52-55

DISCRIMINATION REVERSAL AFTER LATERAL FRONTAL LESIONS IN MONKEYS[1]

CHARLES G. GROSS

Psychophysiological Laboratory, Massachusetts Institute of Technology

Monkeys impaired on delayed response following midlateral frontal lesions, control operatees, and unoperated Ss were tested on 2 discrimination reversals. In Experiment 1 Ss were repeatedly tested for reversal of a discrimination within a session and retention of the same discrimination over 24 hr. Each reversal phase and each retention phase consisted of 30 trials. The frontal operatees made more errors than the other Ss in the reversal phases but not in the retention phases. In Experiment 2 Ss were trained to reverse a previously well-established visual habit. The groups overlapped on this task; each required a mean of over 100 trials to reach criterion. The results suggest that midlateral frontal lesions produce a discrimination deficit that is inversely related to the number of trials per problem.

In the macaque, frontal lesions which include *sulcus principalis* severely impair performance on delayed response tasks. This type of lesion also produces impairment on certain visual discrimination and discrimination reversal tasks. In two discrimination reversal studies in which the number of trials per reversal was small and a simultaneous discrimination training procedure was used, frontal operatees were inferior to normals (Harlow & Dagnon, 1943; Settlage, Zable, & Harlow, 1948). In two other discrimination reversal studies in which the number of trials per reversal was much larger and a successive discrimination procedure was used, sulcus principalis operatees were similar to controls (Gross, 1963; Gross & Weiskrantz, 1962). Frontal lesions which include sulcus principalis have often been reported to impair visual discriminations given for a few trials in a single test session (e.g., Harlow & Dagnon, 1943; Harlow & Settlage, 1948) but not to impair more difficult visual discriminations trained over a number of days (e.g., Gross, 1963; Mishkin & Weiskrantz, 1958; Pribram, 1955; Pribram & Mishkin, 1955; Riopelle, Harlow, Settlage, & Ades, 1951). Similarly, electrical stimulation in the region of sulcus principalis that impairs delayed alternation performance seems to interfere with the learning of simple visual discriminations but not of more difficult ones (Weiskrantz, Mihailovic, & Gross, 1962).

This evidence suggests that frontal lesions may produce a deficit on discrimination tasks that is inversely related to the number of trials per problem. In order to test this hypothesis, sulcus principalis operatees, operated controls, and unoperated controls were compared on two visual discrimination reversal tasks. Experiment 1 involved repeated reversal of a pair of cues with a relatively small number of trials per reversal; Experiment 2 involved reversal of a previously overtrained discrimination.

EXPERIMENT 1

Method

Subjects and apparatus. The *Ss* were nine immature *Macaca mulatta*. Three (No. 10, 30, 38) had received ablations of the banks and depths of sulcus principalis (P group); three (No. 1, 7, 32) had received ablations of the anterior bank of the arcuate sulcus and of rostral tissue on the lateral surface excluding sulcus principalis and served as operated controls (NP group); three (No. 6, 8, 31) were unoperated controls (U group). All *Ss* had

[1] This report is abstracted from a doctoral dissertation submitted to the University of Cambridge in 1961. The experiments were conducted at the University of Cambridge during the author's tenure of a National Institutes of Health Predoctoral Fellowship. The author would like to thank Lawrence Weiskrantz for performing the surgery and for his assistance, interest and advice. This research was supported by the Air Research and Development Command, United States Air Force, through its European Office under Contract AF 61(052)-185 to L. Weiskrantz. Preparation of this report was aided by a National Institutes of Health Postdoctoral Fellowship and National Institute of Mental Health Program Grant M-5673 to H.-L. Teuber.

TABLE 1
SUMMARY OF INDIVIDUAL SCORES

Measure	U Group			NP Group			P Group		
	6	8	31	1	7	32	10	30	38
Experiment 1									
Reversal errors	272	232	208	163	264	261	307	266	281
Retention errors	238	193	163	99	226	164	169	155	207
Experiment 2									
Trials to criterion	210	129	9	120	364	81	297	75	97
Errors to criterion	80	56	6	52	124	32	112	25	50

received identical test experience in delayed alternation, delayed response, auditory discrimination, visual discrimination and reversal and locomotor activity studies. At the time of the present study (about 3 mo. after operation), the delayed alternation and delayed response performance of the P group was severely impaired and the NP group performed as well as the U group. Surgical methods and reconstructions of the lesions have been reported (Gross, 1963).

Testing was conducted in the Wisconsin General Test Apparatus described previously (Gross, 1963).

Procedure. Two pieces of scrap metal differing slightly in color, size, and shape were the discriminanda used throughout this experiment. They were presented simultaneously, one on each of the metal plaques covering the two foodwells. The spatial position of the objects was changed from trial to trial on a schedule derived from a table of random numbers. Placement of food under one object was designated as Condition A and food under the other object as Condition B. On the first day, A was given for 30 trials, followed by B for 30 trials. On the following day B was given for 30 trials, followed by A for 30 trials. This pattern was continued for 20 days and may be summarized as $A_1B_1/B_2A_2/A_3B_3/\ldots/B_{20}A_{20}$, where the numerals refer to successive daily test sessions. Thus, reversal within a session, as well as retention over 24 hr. of the same discrimination, was repeatedly tested. A noncorrection procedure was used.

Results

The performance of the animals is summarized in Table 1. The P group did not make significantly more *total* errors than the control animals (Mann-Whitney Test, $U = 9$, $p = .548$). On the *reversal* phases, the P group made both more errors ($U = 1$, $p = .024$) and a greater proportion of total errors than the other groups ($U = 2$, $p = .048$), the p values being given for a one-tailed test in each case. Thus, on the *retention* phases, the P group made a significantly smaller proportion of its total errors than the other groups, although it did not make a significantly smaller absolute number of errors ($U = 8$, $p = .452$). It was interesting that the P S whose distribution of errors was most similar to that of the U and NP groups, namely No. 38, was also the monkey that (*a*) showed the smallest delayed response deficit, and (*b*) had had least tissue removed from the depths of sulcus principalis (Gross, 1963).

As may be seen in Figure 1, the P group did not make consistently more errors than the other groups in the reversal phases until after the sixth reversal. Since the P and U groups made almost the same number of total errors from this point on, it is possible to compare their intrasession distributions of errors. As may be seen in Figure 2, in the reversal phases after the initial few trials, the P group made more errors than the U group, but the groups were about the same by the end of the session. However, in the first half of each retention phase, the U group made slightly more errors than the

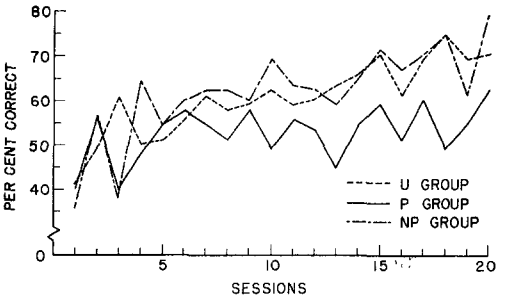

FIG. 1. Mean percentage of correct responses in successive *reversal* phases.

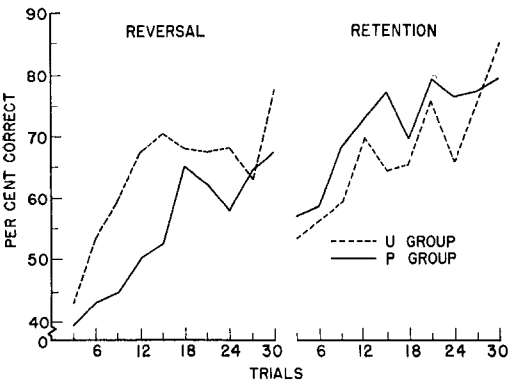

FIG. 2. Mean *intrasession* performance in Sessions 6–20.

P group, but again, the groups overlapped at the end of the session.

EXPERIMENT 2

Method

Subjects and apparatus. The *Ss* and apparatus were the same as in Experiment 1. The P group was still severely impaired on delayed response tasks.

Procedure. Before operation all *Ss* had learned to discriminate a yellow plastic salt cellar (positive cue) from a blue wooden block (negative cue), simultaneously presented. The *Ss* were retrained on this task following operation. There were no significant differences among the groups before or after operation (Gross, 1963). On a subsequent test of retention of this discrimination, all *Ss* reached criterion (45 correct responses in 50 consecutive trials) in the first 50 trials. In the present experiment, the positive cue of this previously learned discrimination became the negative cue, and the previously negative cue was now the positive cue. The *Ss* were tested on this discrimination reversal for 100 trials per day to criterion of 45 correct responses in 50 consecutive trials. A noncorrection procedure was employed. The spatial position of the objects was changed from trial to trial on a schedule derived from a table of random numbers.

Results

As may be seen in Table 1, there were no significant or suggestive differences among the groups in number of trials or errors to criterion. All the *Ss* except No. 31 were tested for more trials on this task than in the studies cited above which reported discrimination reversal impairment after frontal lesions. Similarly, the mean number of trials required to reach criterion was within the range of trials needed to reach criterion on those visual discrimination tasks which in previous studies were found to show no impairment after frontal lesions. By contrast, the mean number of trials needed by the present *Ss* exceeded the number of trials per problem involved in the studies cited above which found a frontal impairment on discrimination tasks.

DISCUSSION

The absence of any deficit of the P group on the discrimination reversal in Experiment 2 indicates that the discrimination reversal procedure per se is not sufficient to reveal impaired performance of delayed response-deficient frontal operatees. The inferior performance of the P group on the short discrimination reversals in Experiment 1 supports the proposed hypothesis that sulcus principalis lesions produce a discrimination impairment which is inversely related to the number of trials per problem.

The results of Experiments 1 and 2 may be open to another explanation. Since Experiment 2 was only a single reversal and the frontal deficit in Experiment 1 appeared only after a number of reversals, it is possible that the principalis operatees have a difficulty in acquiring reversal learning sets regardless of the number of trials per problem. However, if the P group were acquiring a discrimination reversal set more slowly, the differences between it and the other groups might be expected to become progressively greater. But, after the sixth reversal, there was no indication of any increasing differences among the groups. Similarly, in the previous reports of discrimination reversal impairment after frontal lesions (Harlow & Dagnon, 1943; Settlage et al., 1948), there was no tendency for this impairment to increase with successive reversals. A recent experiment by Pribram (1961) also supports the proposed hypothesis and fails to support its alternative. Pribram found no increasing differences between lateral frontal operatees and controls in blocks of discrimination reversals in which the number of correct trials required to attain criterion remained constant. However, he found the frontal operatees increasingly inferior to controls on successive

blocks in which the required number of correct trials on each reversal (and thus the number of trials per reversal) was reduced.

The intrasession distribution of errors in Experiment 1 offers a possible basis for the difficulty of the P group. In the first half of each reversal session, the P animals were severely impaired, but by the end, they were doing as well as the normals. This suggests that they were unable to benefit from their experiences as quickly as the controls but were eventually able to do so. On the first half of each retention session, the P group did slightly better than the normals, suggesting that they were using the (older) information from the previous phase more effectively than did the normal controls.

The tasks on which sulcus principalis lesions have the greatest effect, namely delayed response and delayed alternation, may be viewed as the limiting cases of decreasing trials per problem; they are one trial discrimination (or discrimination reversal) problems (Nissen, Riesen, & Nowlis, 1938). It is thus possible that the delayed-response deficit and the deficit on "short" discrimination tasks have a common basis. As discussed elsewhere (Gross, in press), the present hypothesis is compatible with an explanation of the frontal deficit in terms of a recent memory deficit (Jacobsen, 1936) or an increased perseveration or other error tendency (Lawicka & Konorski, 1962; Mishkin, Prockop, & Rosvold, 1962; Settlage et al., 1948).

REFERENCES

Gross, C. G. A comparison of the effects of partial and total lateral frontal lesions on test performance by monkeys. *J. comp. physiol. Psychol.*, 1963, **56**, 41–47.

Gross, C. G. Some changes in behavior produced by lateral frontal lesions in the macaque. In K. Akert and J. M. Warren (Eds.), *The prefrontal cortex and behavior*. in press.

Gross, C. G., & Weiskrantz, L. Evidence for dissociation of impairment on auditory discrimination and delayed response following lateral frontal lesions in monkeys. *Exp. Neurol.*, 1962, **5**, 453–476.

Harlow, H. F., & Dagnon, J. Problem solution by monkeys following bilateral removal of the prefrontal areas: I. Discrimination and discrimination reversal problems. *J. exp. Psychol.*, 1943, **32**, 351–356.

Harlow, H. F., & Settlage, P. Effect of extirpation of frontal areas upon learning performance of monkeys. *Res. Publ. Ass. Nerv. Ment. Dis.*, 1948, **27**, 446–459.

Jacobsen, C. F. Studies of cerebral function in primates: I. The functions of the frontal association areas in monkeys. *Comp. Psychol. Monogr.* 1936, **13**, 3–60.

Lawicka, W., & Konorski, J. Analysis of the impairment of delayed response after prefrontal lesions. In E. Gutman (Ed.), *Central and peripheral mechanisms of motor behavior*. Liblice, Czechoslovakia: 1962.

Mishkin, M., Prockop, E. S., & Rosvold, H. E. One-trial object discrimination in monkeys with frontal lesions. *J. comp. physiol. Psychol.*, 1962, **55**, 178–181.

Mishkin, M., & Weiskrantz, L. Effects of delaying reward on visual-discrimination performance in monkeys with frontal lesions. *J. comp. physiol. Psychol.*, 1958, **51**, 276–281.

Nissen, H. W., Riesen, A. H., & Nowlis, V. Delayed response and discrimination learning by chimpanzees. *J. comp. Psychol.*, 1938, **26**, 361–368.

Pribram, K. H. Toward a science of neuropsychology (method and data). In, *Current trends in psychology and the behavioral sciences*. Pittsburgh, Pa.: Univer. Pittsburgh Press, 1955. Pp. 115–142.

Pribram, K. H. A further experimental analysis of the behavioral deficit that follows injury to the primate frontal cortex. *Exp. Neurol.*, 1961, **3**, 432–466.

Pribram, K. H., & Mishkin, M. Simultaneous and successive visual discrimination by monkeys with inferotemporal lesions. *J. comp. physiol. Psychol.*, 1955, **48**, 198–202.

Riopelle, A. J., Harlow, H. F., Settlage, P. H., & Ades, H. W. Performance of normal and operated monkeys on visual learning tests. *J. comp. physiol. Psychol.*, 1951, **44**, 283–289.

Settlage, P., Zable, M., & Harlow, H. F. Problem solution by monkeys following bilateral removal of the prefrontal areas: VI. Performance on tests requiring contradictory reactions to similar and to identical stimuli. *J. exp. Psychol.*, 1948, **38**, 50–65.

Weiskrantz, L., Mihailovic, L., & Gross, C. Effects of stimulation of frontal cortex and hippocampus on behaviour in the monkey. *Brain*, 1962, **85**, 487–504.

(Received March 6, 1962)