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A COMPARISON OF THE EFFECTS OF PARTIAL AND TOTAL LATERAL FRONTAL LESIONS ON TEST PERFORMANCE BY MONKEYS[1]

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3 monkeys with sulcus principalis lesions (P group), 3 with lateral frontal lesions sparing sulcus principalis (NP group), 3 with total lateral frontal lesions (T group) and 3 unoperated Ss (U group) were compared on retention of simultaneous visual discrimination and acquisition of (a) delayed alternation, (b) auditory discrimination, (c) 2 successive visual discriminations, and (d) discrimination reversal. The groups did not differ on the visual tasks. On alternation both the P and T groups were severely impaired, the T group being poorer. On auditory discrimination only the T group was markedly impaired. Alternation results lend themselves to a focus-field description. Both focus-field and mass action descriptions are consistent with the auditory discrimination findings.

Lesions of granular cortex on the lateral aspect of the frontal lobe are consistently followed by the delayed response deficit but cortical lesions elsewhere in the frontal lobe are not (Pribram, 1955b; Pribram, Kruger, Robinson, & Berman, 1955). Within lateral frontal cortex, lesions of *sulcus principalis* result in a severe impairment on delayed alternation (Mishkin, 1957) and delayed response tests (Gross & Weiskrantz, 1962), but larger lesions elsewhere on the lateral frontal surface result in a mild deficit which disappears with time and training, time alone probably being sufficient (Gross & Weiskrantz, 1962; Pribram, 1955a). These findings cannot be described in terms of mass action (even applied in a circumscribed cortical region). Nor are they consistent with a view of a discrete cortical lesion having a specific all-or-none effect on the delayed response task. One alternative characterization is in terms of a *focus* and a *field.* The focus of a deficit is that tissue ablation of which results in the greatest deficit per unit mass removed. If ablation of adjacent tissue is followed by a smaller deficit this region is termed the field of the deficit (Chow & Hutt, 1953; Gross & Weiskrantz, 1962).

To test the applicability of this characterization to the delayed response-type deficit, monkeys with (*a*) no lesion (unoperated or U group), (*b*) ablation of sulcus principalis alone (principalis or P group), (*c*) ablation of lateral frontal cortex sparing sulcus principalis (nonprincipalis or NP group), and (*d*) ablation of the entire lateral frontal cortical surface (total lateral frontal or T group) were compared in their performance of delayed alternation. The focus-field model predicts the following rank order of increasing impairment on delayed alternation: U < NP < P < T.

These same four groups of monkeys were also taught an auditory discrimination in order to (*a*) confirm the previous reports of a deficit on auditory discrimination following lateral frontal lesions, (Blum, 1952; Weiskrantz & Mishkin, 1958; Rosvold & Mishkin, 1961), (*b*) confirm the previous report of dissociation between the delayed response and auditory discrimination impairments (Gross & Weiskrantz, 1962), and (*c*) compare the effect of different lateral frontal lesions on performance of this task.

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Either a mass action hypothesis or a focus-field hypothesis with the focus other than sulcus principalis would predict the following rank order of increasing impairment on auditory discrimination, P < NP < T, or, if the size of the sulcus principalis lesion is above the minimum lesion followed by an auditory discrimination deficit, U < P < NP < T.

The *S*s were also compared on the performance of visual discriminations in order to determine the behavioral specificity of the effects of the three varieties of frontal lesions.

Method

Subjects

The *S*s were 13 experimentally naive, immature *Macaca mulatta*. They entered the laboratory 3 to 6 weeks before training began and their weights at the time of operation ranged from 1.7 to 2.2 kg. Three *S*s (No. 10, 30, and 38) received bilateral ablations of the banks and depths of sulcus principalis (P group). Three *S*s (No. 1, 7, and 32) received bilateral ablations of the depths and anterior bank of the arcuate sulcus and of rostral cortex on the lateral surface except for the banks and depths of sulcus principalis (NP group). Three *S*s (No. 34, 36, and 37) received bilateral ablations of the entire lateral frontal surface—from the depths of the arcuate sulcus to the frontal pole and including sulcus principalis (T group). Three *S*s (No. 6, 8, and 31) were unoperated controls (U group). The thirteenth *S* (No. 4) had been intended for the P group, but when his brain was examined at the time of sacrifice it was discovered that only the anterior half of sulcus principalis had been ablated.

Coincident with this study, the locomotor activity of these *S*s under various stimulus conditions was investigated (Gross, 1963).

Surgery and Histology

Surgical[2] and histological procedures were the same as in an earlier study (Gross & Weiskrantz, 1962). Reconstructions and sample cross sections of the lesions are shown in Figures 1 and 2.

Apparatus

All testing was conducted in a modified Wisconsin General Test Apparatus. The testing space measured 26 x 16 x 27½ in. Two 40 w. strip lights were mounted in the top of the transport cage compartment and two in the top of the testing space. A 2½ in. speaker was mounted downward in the roof of the testing space. The testing space contained a platform 6 x 26 x 2 in. with three foodwells (diameter 1½ in., maximum depth ½ in., 7¼ in apart) which could each be covered by a metal plaque 3½ x 3½ in. In object discriminations, the discriminada were placed on these plates. The two side foodwells were used in two-choice tasks. In successive ("go-no go") discriminations only the center foodwell was used and the "no go" reward was delivered in a metal cup (diameter 1½ in., depth ½ in.) attached to a metal rod.

Procedure

The *S*s received about 200 gm. of chow each day, after testing. A single raisin per trial was the incentive used throughout.

Each *S* was subjected, successively, to the following procedures:

Experiment 1a. Simultaneous object discrimination, acquisition. The discriminanda were a yellow plastic salt cellar (positive) and a blue wooden block (negative). Both were presented simultaneously on each trial, one over each of the plaques covering the side foodwells. *S*s were trained for 30 trials per day to a criterion of 45 correct trials out of 50 consecutive trials (abbreviated hereafter as 45/50).

Operation and 14 day Recovery Period: Experiment 1b. Simultaneous object discrimination, retention. *S*s were tested for retention of the discrimination learned in Experiment 1a for 30 trials per day to a criterion of 45/50.

Experiment 2. Go-no go auditory discrimination, acquisition. The positive stimulus was white noise; its intensity in the transport cage was 68 db. The negative stimulus was a 1,000 cps tone; its intensity in the transport cage was 67.5 db. Both sounds were delivered from the speaker in the roof of the testing space. Five seconds after the sound stimulus was turned on, the opaque screen was raised for a further 5 sec. period during which *S* faced a plaque over the central foodwell. If it displaced the plaque within this 5 sec. period when the positive stimulus was on, it found a raisin under it. Conversely, if it refrained from responding in this period when the negative stimulus was on it received a raisin via the metal cup and rod described above. If *S* either displaced the plaque when the negative stimulus was on, or did not displace it when the positive stimulus was on, it did not receive any food during that trial. The stimulus was turned off and the opaque screen lowered after the plaque was displaced, or at the end of the 5 sec. period, whichever came first. *S*s were tested for 50 trials per day to a criterion of 90/100.

Experiment 3. Delayed alternation, acquisition. On the initial trial of each session both side foodwells were baited, the plaques placed over the foodwells and the opaque screen raised. Immediately after the animal responded, the opaque screen was lowered, the plaques replaced, and after an interval of 3 sec. it was raised again. During each subsequent 3 sec. interval, the foodwell opposite to the one which *S* had selected on the previous trial was baited and both plaques replaced. Thus the *S* would receive a raisin each

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[2] The author would like to thank L. Weiskrantz and K. Pribram for performing almost all the surgery. The former operated on No. 1, 4, 7, 10, 30, 32, and 34; the latter operated on No. 36 and 37.

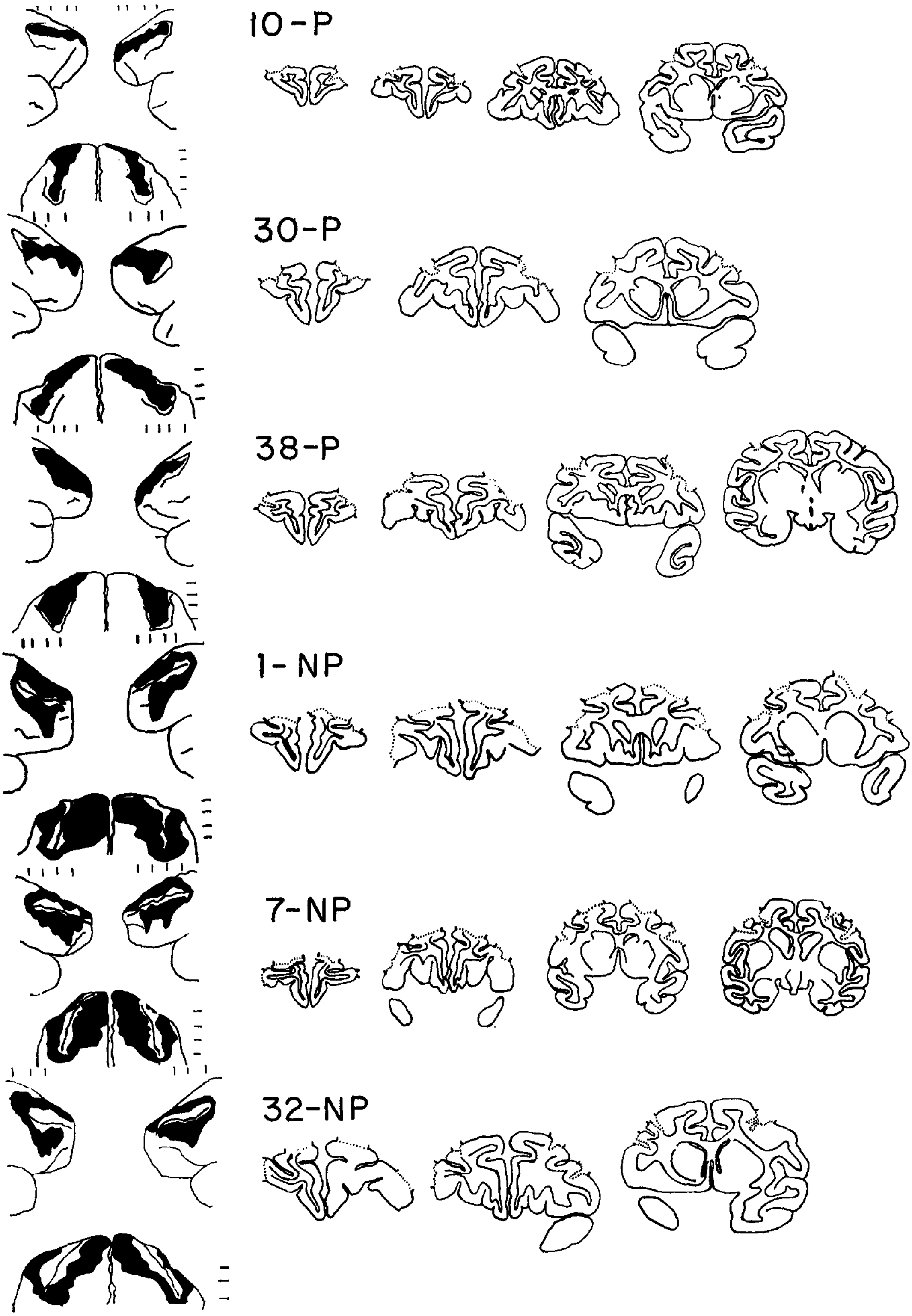

FIG. 1. Lateral and dorsal reconstructions of the lesions (left panel) and cross sections through the lesions (right panel) of the *Principalis* (P) and *Nonprincipalis* (NP) groups. (Black in the reconstructions and dotted lines in the cross sections indicate damage. The cross sections correspond to the anterior-posterior levels marked on the reconstructions.)

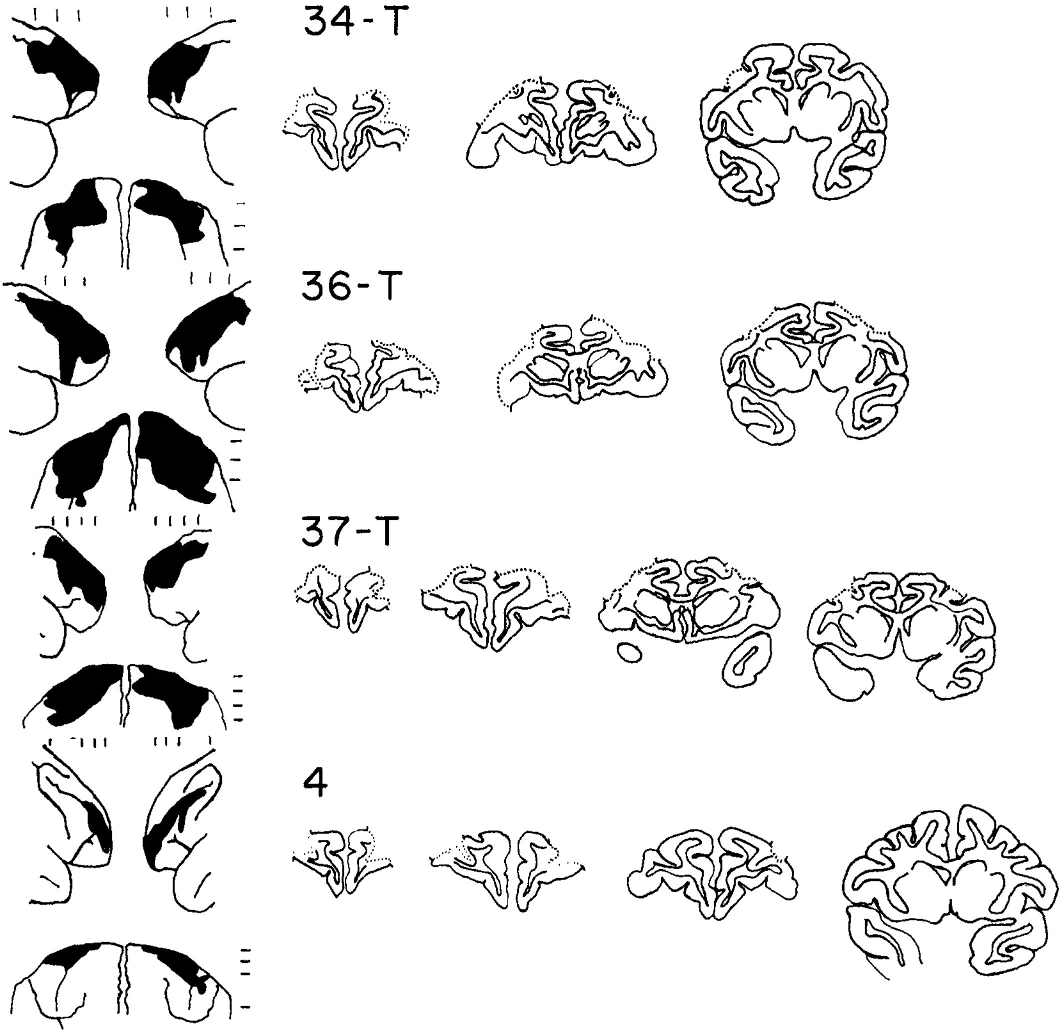

FIG. 2. Lateral and dorsal reconstructions (left panel) and cross sections through the lesions (right panel) of the Total (T) group and No. 4 (See legend to Fig. 1.)

time it alternated its response from trial to trial. *S*s were tested for 50 trials per day (excluding the initial trial on which they could not err) to a criterion of 90/100 or a maximum of 1,650 trials.

Experiment 4. Simultaneous object discrimination, retention. *S*s were again tested for retention of the discrimination learned in Experiment 1a for 30 trials per day to a criterion of 45/50.

Experiment 5. Go-no go object discrimination, acquisition. The positive discriminandum was a red plastic jar cover and the negative one was a piece of green scrap metal. On each trial, *S* faced a single discriminandum placed on the plaque covering the central foodwell. If *S* displaced the plaque under the positive cue within 5 sec., it found a raisin in the foodwell; if it refrained from displacing the plaque under the negative cue, it received a raisin via the metal cup and rod mentioned above. If it either displaced the plaque under the negative cue or did not displace the plaque under the positive cue within the 5 sec. period, it did not receive any food on that trial. The screen was lowered at the end of 5 sec., or after *S*s responded, whichever came first. *S*s were trained for 50 trials per day to a criterion of 90/100 or a maximum of 600 trials.

Experiment 6. Go-no go pattern discrimination, acquisition. The positive discriminandum was a red "x" painted on a light green plaque 4 x 3½ in., and the negative one was a red diamond painted on a similar plaque. The procedure was identical to that of Experiment 5 except that one of the two discriminanda replaced the plaque covering the central foodwell on each trial.

Experiment 7. Go-no go object discrimination reversal. The procedure was identical to that of Experiment 5 except that the positive stimulus of

Experiment 5 was the negative stimulus and the negative stimulus was the positive one, i.e., the positive stimulus was now the piece of green scrap metal and the negative stimulus was now the red plastic jar cover.

In the auditory discrimination (Experiment 2) the intertrial interval was 5 sec. and in the visual discriminations (Experiments 1, 4–7) it was at least 10 sec. Correction trials were never used and self-correction within the trial was not allowed. Except on the delayed alternation test, stimuli were presented on each trial according to a predetermined balanced order, regardless of whether or not *S* was correct.

Results

The Kruskal-Wallis (1952) test was used to test for overall difference among the groups, Jonckheere's (1954) distribution-free *k*-sample test against ordered alternatives was used to test predictions of specific rank orders of the groups, and the Mann-Whitney (1947) test was used to test intergroup differences.

Visual Discriminations

On the simultaneous object discrimination (Experiment 1), there were no significant differences among the groups in savings ratios (Kruskal-Wallis test, $H = 1.5$). On the second retention test of this discrimination (Experiment 4), all *S*s reached criterion in 50 trials. Neither the go-no go object discrimination (Experiment 5) nor the go-no go pattern discrimination (Experiment 6) yielded any significant differences among the groups in trials or errors to criterion ($H < 3.4$ in all cases). However, on the object discrimination the T group was slightly but not significantly superior to all other *S*s, and on the pattern discrimination one *S* from each group except the T group was still performing at chance level at the end of 600 trials. On the reversal of the go-no go object discrimination (Experiment 7) the groups also did not differ significantly in trials or errors to criterion ($H = 0.5$; $H = 0.3$). Nevertheless it was interesting that 2 NP, 1 P, and 1 T monkey but no U monkey failed to learn this reversal in the allotted 300 trials. On none of the visual discrimination tasks did any two groups differ significantly (Mann-Whitney test, $U > 0$ in all cases). See Table 1.

On all the visual tasks *S*s made a far greater proportion of no-go errors than go errors and the different groups did not differ with respect to this ratio.

Delayed Alternation

On the delayed alternation experiment (Experiment 3) the null hypothesis may be rejected and the rank order of increasing deficit predicted by the focus-field hypothesis, namely U < NP < P < T, accepted with considerable confidence for both trials and errors (Jonckheere's, $S = 44$, $p = .00047$; $S = 42$, $p = .00093$). Comparison of adjacent groups with a one-tailed Mann-Whitney test indicates the T group to be more impaired than the P group ($U = 0$, $p = .05$) and the P group to be more impaired than the NP group ($U = 0, p = .05$). The NP and U groups did not differ significantly. See Table 1.

The P animal that performed best on this task (No. 38) had more tissue remaining in the depths of sulcus principalis and a larger total lesion than the other P animals. The *S* that had sustained an ablation of only the anterior half of sulcus principalis (No. 4) took more trials to reach criterion (706) than the mean of the U group (477) or of the NP group (620), but performed very much better than either of the other groups.

Auditory Discrimination

In the auditory discrimination experiment, the null hypothesis may be rejected and the hypothesis of increasing deficit in the order P < NP < T may be accepted. (Jonckheere's test, $S = 19$, $p = .0208$ for trials and $S = 17, p = .0369$ for errors). The U and P groups learned the task at about the same rate and the alternative hypothesis of increasing deficit in the order U < P < NP < T fails to reach significance ($S = 22$ for trials and $S = 24$ for errors). The performance of no two individual groups differed significantly but the group with the largest lesions (T group) was significantly poorer on this task than all the other *S*s combined (one-tailed Mann-Whitney test for trials, $U = 4, p < .05$; for errors, $U = 3, p < .025$). See Table 1.

The lesion of the most impaired P animal on this task (No. 38), as noted above, par-

TABLE 1
PERFORMANCE OF INDIVIDUAL *S*s

Experiment	U Group			P Group			NP Group			T Group			
	6	8	31	10	30	38	1	7	32	34	36	37	4
1. Simultaneous object discrimination (retention)	.55	−.35	.59	−.41	.19	.65	.13	.64	1.00	−.12	.30	.59	.83
2. Auditory discrimination	896 (278)	1598 (719)	1108 (510)	895 (307)	893 (309)	1252 (599)	1261 (541)	1437 (548)	921 (325)	1775 (809)	2716 (1309)	1177 (543)	1054 (409)
3. Delayed alternation	778 (285)	293 (127)	360 (100)	1650 F (435)	1409 (471)	797 (242)	708 (214)	703 (189)	449 (120)	1650 F (547)	1650 F (684)	1650 F (466)	706 (231)
5. Successive object discrimination	49 (19)	95 (38)	46 (16)	280 (99)	108 (52)	0 (0)	18 (10)	141 (56)	80 (31)	10 (6)	7 (2)	22 (12)	32 (17)
6. Successive pattern discrimination	600 F (275)	97 (37)	112 (52)	600 F (262)	402 (297)	376 (138)	267 (101)	301 (126)	600 F (288)	434 (176)	284 (108)	208 (67)	203 (77)
7. Successive object discrimination reversal	201 (83)	194 (93)	250 (124)	240 (122)	198 (38)	300 F (189)	64 (42)	300 F (172)	300 F (176)	219 (115)	300 F (199)	69 (49)	300 F (181)

Note.—The measure for Experiment 1 is one of savings, viz. $\frac{\text{pre-op. trials to criterion} - \text{post-op. trials to criterion}}{\text{pre-op. trials to criterion} + \text{post-op. trials to criterion}}$.
All other figures are trials (and errors) required to attain criterion. "F" indicates failure to attain criterion in the stated trials. (The corresponding error score is the number of errors made during these trials.)

tially spared the depths of sulcus principalis and included a larger area of tissue than any other P lesion. The performance of *S* that had received the very small principalis lesion (No. 4) was similar to that of the P and U groups.

As in the visual go-no go tasks, all *S*s made a greater proportion of no-go errors than go errors, and this measure did not differ among the groups.

DISCUSSION

The difficulty of the various visual discrimination tasks (i.e., the number of trials required by the controls to reach criterion) was less than the difficulty of the delayed alternation and auditory discrimination tasks. Nevertheless, the failure of the visual tasks to discriminate between the groups strongly suggests that on neither the alternation nor the auditory task were the results due to a nonspecific deterioration in learning or performance. This suggestion is reinforced by the slightly better performance of the T group on two of the visual tasks (the T *S*s were the poorest performers on the auditory and delay tasks.)

The results on the delayed alternation test confirm the previous finding (Mishkin, 1957) that lesions of sulcus principalis result in a greater delayed alternation deficit than lesions of equal size elsewhere; in addition, they indicate (*a*) that lesions of sulcus principalis produce much greater deficits than larger lesions of surrounding tissue on the lateral surface and (*b*) that lesions of the entire lateral surface yield a greater delayed alternation deficit than sulcus principalis lesions alone. In other words, sulcus principalis may be called the focus of the deficit; the surrounding tissue on the lateral surface of the frontal lobe may be called the field of the deficit, and the impairment following combined focus and field lesions is greater than that following focus lesions alone. Furthermore, destroying the banks of sulcus principalis and sparing most of the depths *or* destroying the banks and depths of the anterior half of sulcus principalis resulted in a much smaller alternation deficit than complete ablation of the banks and depths of sulcus principalis.

The superior performance of the P group on the auditory discrimination confirms the previous report (Gross & Weiskrantz, 1962) that the delayed response and auditory discrimination deficits may be dissociated. The failure to find any difference between the unoperated controls and the P group suggests that if sulcus principalis is in the field of the auditory discrimination deficit, it is below the critical mass which must be removed in order to produce impairment on auditory discrimination.

The results of the previous study (Gross & Weiskrantz, 1962) suggested that the frontal delayed response and auditory discrimination deficits may be *doubly* dissociated; that is, *S*s with sulcus principalis lesions were relatively impaired on delayed response, but not on auditory discrimination, and *S*s with lateral frontal lesions sparing sulcus principalis were relatively impaired on auditory discrimination but not on delayed response. However, in the present experiment one P animal learned the auditory discrimination more slowly than one NP animal and the difference between the P and NP groups was nonsignificant and smaller than in the previous study. Thus the present results only support *single* dissociation of the two deficits. This apparent difference between the two studies may be related to the considerably younger age of the *S*s in the present study since cerebral insult seems to have less effect on young mammals than on older ones (e.g., Akert, Orth, Harlow, & Schiltz, 1960; Benjamin & Thompson, 1959). The smaller difference between the T group and the U group in this study than in previous ones (Rosvold & Mishkin, 1961; Weiskrantz & Mishkin, 1958) may also have been related to this age factor.

Additional experiments are required to establish the reality of double dissociation of the frontal auditory discrimination and delayed response deficits and the possible relevance of age to their production and dissociation. The present auditory discrimination results are equally consistent with a focus-field description (with the focus other than sulcus principalis) and a mass action description. Comparisons of the effect of equal size lesions of frontal and other cortex on this task should help distinguish between these two possibilities.

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