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EFFECTS ON DELAYED-RESPONSE PERFORMANCE OF LESIONS OF DORSOLATERAL AND VENTROMEDIAL FRONTAL CORTEX OF BABOONS

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It has been well established that gross damage to the frontal lobes produces severe disturbance of monkeys' performance on delayed-response–type test (2, 5, 11). However, there is little information relating the topographic organization of frontal cortex to such disturbance except that resection limited to the precentral "motor" areas does not produce this alteration in behavior (6). The present experiments were designed to determine whether the integrity of a restricted portion of the frontal lobe anterior to the precentral "motor" areas is especially important for performance on delayed-response–type tasks.

Data obtained by the method of strychnine neuronography were chosen to guide surgical removals (15). Neuronographically, the frontal cortex, exclusive of the motor areas, is divisible into three sections, the core of each being a region within which all points are related by reciprocal connections. These sections are referred to as (*a*) dorsolateral, (*b*) ventromedial, and (*c*) ventrolateral. The ventrolateral section is part of a more extensive segment extending to the temporal polar formation and into the island of Reil, and the behavioral effects of ablations restricted to this segment are to be reported elsewhere (13).

The present report deals, therefore, with a comparison of the behavioral effects of bilaterally symmetrical lesions of the other two neuronographically defined sections of frontal cortex: the dorsolateral and the ventromedial.

PROCEDURE

Subjects

Nine guinea baboons (*Papio papio*) were arbitrarily divided among the experimenters for the purpose of preoperative training. They were then placed in three experimental groups matched on the basis of weight, each group containing three animals numbered 1 to 3, weighing approximately 4, 6, and 9 kg., respectively. The groups will be designated C for nonoperate controls, DL for dorsolateral operates, and VM for ventromedial operates. Postoperatively, the animals were rearranged into three testing groups, each group containing three animals of equal weight and hence one animal from each of the three experimental groups. Each of the three testing groups was then assigned to a different experimenter.

Soon after completing Phases I and II of the postoperative testing schedule, VM1 died of an acute gastrointestinal illness. C2, after serving as a control animal for these two phases, was operated upon (VM4) to replace her. He then received the complete postoperative testing schedule, increasing to 4 the *N* of the VM group for Postoperative Phases I and II.

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Surgical Procedures

Animals in groups DL and VM were operated alternately. Under intraperitoneal sodium-amytal anesthesia (approximately 0.6 cc/kg body weight) a linear scalp incision was made extending from one temporal region to the other across the vertex. A full calvarium osteoplastic flap was then turned on the left temporal bone, exposing both cerebral hemispheres forward of the central sulcus. The dura was opened bilaterally in all instances, but for the ventromedial lesions the dura was opened only minimally on the right, and on the left several (usually 2 to 3) small veins near the saggital sinus were interrupted with electrocautery. The cortex was subpially resected in scar-minimizing fashion with an 18 gauge metal sucker designed for the purpose. Symmetrical bilateral removals were performed in one stage, and white matter was not intentionally invaded. The dorsolateral lesions extended from the arcuate sulcus forward to the pole, and included the depths of the *sulcus principalis*. The ventromedial lesions included the medial aspect of the pole and the medial orbital, anterior cingulate, and subcallosal gyri. The depths of the subcallosal (rostral) sulcus were invaded, but those of the callosomarginal sulcus were spared. Wounds were closed in anatomical layers with silk.

Tests

In addition to receiving delayed-response training the animals were tested on delayed-alternation and visual-discrimination problems. The alternation task was administered only postoperatively in order to determine the effects of frontal lobe damage on the initial acquisition of a delayed-response–type habit. The visual-discrimination problem was presented both pre- and postoperatively in order to measure the retention of a habit not closely related to delayed response. Throughout the experimental period systematic observations were made of the animals' general behavior, and postoperatively quantitative estimates of the animals' locomotor activity were obtained.

Apparatus

A transporting cage was used to move the animal from the individual living quarters to an air-conditioned, soundproofed, darkened testing room. Here the cage was moved into a dimly illuminated enclosure and secured in place facing the opaque screen of the testing apparatus. When the opaque screen was raised, the animal was confronted with a sliding tray to which were attached two rectangular metal cups, spaced 12 in. apart. Metal cup-covers, 3 in. by 4 in., served as interchangeable stimulus plaques, which the animal quickly learned to displace to obtain the concealed reward. Unpainted covers were used for the delayed-response and delayed-alternation tests. Covers bearing an inverted (positive) and an erect triangle painted flat black on yellow backgrounds were used for the visual-discrimination problem. A one-way vision screen separated the animal from the experimenter.

The locomotor activity of the animal was measured in an "activity cage" by means of an RCA capacity-operated relay, grounded to the cage floor and to antennae at both ends. Changes in the antenna capacity, caused by movement of the animal in the field between antenna and ground, activated a counter. The cage was enclosed in an illuminated, ventilated, sound-resistant box.[2]

Testing Procedures

To adapt the animals to the testing situation they were trained on delayed response at the 0-sec. (minimal) interval without the screen. A trial was presented in the following manner: One of the cups was baited with a peanut in full view of the animal, the lids were

[2] The authors are indebted to Dr. George D. Davis for the use of this apparatus, a detailed description of which is to be found in Davis (4).

closed, the one-way vision screen was lowered, the tray pushed forward, and the animal permitted to make a choice. Left and right cups were baited in a predetermined balanced order. The noncorrection technique was employed. No punishment, other than withholding reward, was given for errors. Thirty trials were presented daily until the criterion of 85 correct in 100 consecutive trials was achieved. This training constituted the adaptation period.

The same procedure was then used for the formal tests with the following exceptions. The delayed-response test was presented with the opaque screen interposed for delays of 0-(minimal), 5-, and 10-sec. after baiting; for the visual-discrimination problem, cups were baited with the opaque screen lowered; for delayed alternation, cups were baited with the opaque screen interposed, and 50 trials, separated by 5-sec. delays, were presented by the correction technique. (Because all correction trials were included in the daily total, scores below 50 per cent, indicating consistent left or right position preferences, could be obtained.)

Systematic observations of the animals' behavior were recorded daily before and after operation. These observations embraced kind and degree of (*a*) motility—running, jumping, walking into and out of the transporting cage; pacing, circling, sitting in the transporting cage preceding, during, and following the testing session; (*b*) reactivity—pouncing at the experimenter, slapping or biting the cage, attempts to escape, crouching, defecation, piloerection; and (*c*) vocalization—screaming, barking, chattering.

Postoperatively, six 3-hr. recordings, each on a separate day, were taken of an animal's activity in the "activity cage." Half of each animal's sessions were run in the morning and half in the afternoon. The data for a given subject were averaged to yield an hourly count, each average being based on a total of 18 hr. in the activity cage.

Immediately after each day's testing the animal was returned to its home cage and fed a synthetic biscuit diet designed to provide 70 cal/kg body weight. Vitamin C in cornstarch candy was administered three times a week. Water was always available in the living cage.

Testing Schedule

Preoperatively, following the adaptation period of delayed response, animals were trained on this test to criterion at 0-, 5-, and 10-sec. intervals, successively. They were then trained to criterion on the visual-discrimination task.

Postoperatively, the testing was divided into three phases: retention of preoperatively learned habits (delayed response and visual discrimination); relearning of delayed response; and initial learning of delayed alternation.

Phase I. Two and one-half to three weeks postoperatively the animals were tested for retention of the delayed-response habit at the 10-sec. interval with screen.[a] A maximum of 750 trials was presented, interrupted after the first 300 trials by a retention test for the visual-discrimination habit.

Phase II. Failure on the retention test for delayed response was followed 2 mo. postoperatively by retraining at the 0-sec. interval with screen. Animals that succeeded at this level were retrained through 5- and 10-sec. delays; those that failed (after 750 trials) received retraining to criterion at the 0-sec. interval without screen, and were then given an additional 150 trials at the same delay with screen.

Phase III. Five months postoperatively eight animals (C1, C3; DL1 to 3; VM2 to 4) were trained for initial learning on the alternation problem. A maximum of 1,000 trials was presented. Six months postoperatively the same eight animals were tested in the activity cage.

[a] For the purpose of the present study an animal is considered to have shown partial retention of this habit if, postoperatively, the number of trials and errors it required to attain criterion at the 10-sec. delay was less than the combined number of trials and errors it required initially to attain criterion at all delays. The maximum number of trials presented postoperatively was greater than the total number required initially by the slowest animal.

Anatomical Procedures

Following completion of the behavioral observations the animals were sacrificed by intraperitoneal injection of a lethal dose of Nembutal. The brains were percardially perfused with saline solution followed by 10 per cent formalin. Fixation in several changes of 10 per cent formalin for two weeks was followed by dehydration in ascending concentrations of alcohol. Thin nitrocellulose (1 per cent) and thick celloidin (10 per cent) were used for imbedding. The brains were serially sectioned at 25 mμ, with every tenth section saved and every twentieth section stained with analine thionine. Reconstruction of the lesion was made from every fourth stained section; thalamic degeneration was estimated by microscopic examination in every other stained section. Representative cross sections through the lesion and through the thalamus were made in addition to the reconstruction.

TABLE 1

VISUAL DISCRIMINATION AND DELAYED RESPONSE: PREOPERATIVE LEARNING AND POSTOPERATIVE RETENTION

Scores are trials and errors preceding 85 correct choices in 100 consecutive trials. For delayed response, preoperative trials and errors at 0-, 5-, and 10-second delays are combined into one total score, whereas postoperative trials and errors are for the 10-second delay only. An underlined score denotes inability to attain criterion within the limits of training, final level of performance being indicated by the number correct in the last 100 trials.

SUBJ. NO.	VISUAL DISCRIMINATION				DELAYED RESPONSE				
	Preoperative		Postoperative		Preoperative		Postoperative		
	Trials	Errors	Trials	Errors	Trials	Errors	Trials	Errors	No. Correct Last 100 Trials
C1	790	207	80	36	10	5	110	33	—
C2	230	61	20	8	590	139	0	0	—
C3	750	288	20	3	230	83	250	85	—
VM1	110	35	0	0	630	157	60	18	—
VM2	150	66	10	5	610	161	750	363	56
VM3	290	110	130	61	430	121	750	313	58
VM4	230	61	10	5	590	139	240	75	—
DL1	160	64	140	72	290	95	750	370	57
DL2	540	150	150	75	210	70	750	367	46
DL3	300	128	240	108	590	145	750	352	59

RESULTS

Behavioral Results

Table 1 presents preoperative learning and postoperative retention scores for delayed response and visual discrimination (Phase 1). Considerable overlapping is seen in the preoperative scores of the three experimental groups, with the greatest variability being found in the scores of the nonoperate controls. Postoperatively, whereas there are only exceptional cases of complete retention, an analysis by the method of savings reveals many instances of partial retention. Thus, on the discrimination problem each animal scored fewer than its original number of trials and errors, although the three dorsolateral operates consistently required somewhat more training than the others to reach criterion. Similarly, in the delayed-response retention test some animals achieved a criterion score in fewer trials and errors than they had required initially. Two controls were

TABLE 2

Delayed Response: Postoperative Relearning

Scores are trials and errors preceding 85 correct choices in 100 consecutive trials at several delay intervals, with screen except where indicated. An underlined score denotes inability to attain criterion within the limits of training, final level of performance being indicated by the number correct in the last 100 trials.

SUBJ. NO.	0-SEC.		5-SEC.		10-SEC.	
	Trials	Errors	Trials	Errors	Trials	Errors
VM2	70	14	140	36	250	64
VM3	0	0	0	0	0	0

	0-SEC.			0-SEC. WITHOUT SCREEN		0-SEC.		
	Trials	Errors	No. Correct Last 100 Trials	Trials	Errors	Trials	Errors	No. Correct Last 100 Trials
DL1	600	303	50	240	78	150	68	51
DL2	600	307	42	500	141	150	52	64
DL3	600	304	50	310	178	150	75	50

TABLE 3

Delayed Alternation: Postoperative Initial Learning

Scores are the number correct in the last 100 of each of four consecutive 250-trial blocks.

SUBJ. NO.	TOTAL NO. OF TRIALS PRESENTED	NO. CORRECT			
		1st	2nd	3rd	4th
C1	250	80	—	—	—
C3	1000	56	60	75	71
VM2	1000	52	66	79	73
VM3	1000	54	68	68	73
VM4	1000	60	65	71	71
DL1	1000	40	54	45	44
DL2	1000	39	45	47	53
DL3	1000	28	38	47	32

slightly retarded. However, the three dorsolateral operates and VM2 and VM3 showed no evidence of retention in 750 trials.

Table 2 presents the scores of these last five animals on the delayed-response retraining tests (Phase II). VM2 and VM3 relearned the habit quickly at the 0-sec. interval with screen and then performed successfully at the 5- and 10-sec. delays with little or no further training. In contrast, the three dorsolateral operates failed to relearn within the limits of testing even at the minimal delay with screen, succeeding only at the same delay without screen after prolonged training. Furthermore, these animals showed no evidence of transfer in the final test when the opaque screen was reintroduced.

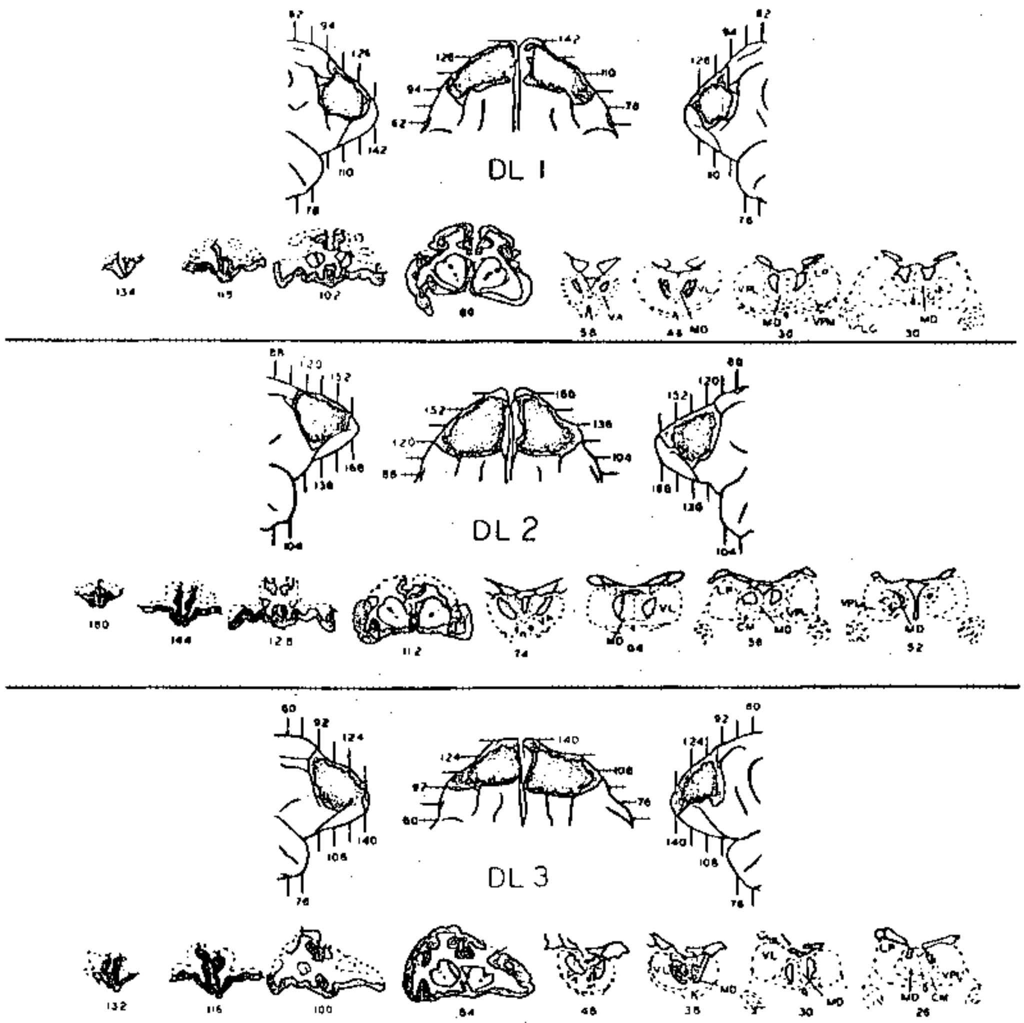

FIG. 1. LATERAL AND DORSAL RECONSTRUCTIONS OF DORSOLATERAL FRONTAL LESIONS

Representative cross sections through lesion and through thalamus shown below reconstruction. Black indicates lesion in the reconstructions, degeneration in the thalamus, and intact cortex in cross sections through the brains. *AM*, *n. anterior medialis; AV*, *n. anterior ventralis; VA*, *n. ventralis anterior; VL*, *n. ventralis lateralis; MD*, *n. medialis dorsalis; VPL*, *n. ventralis posterior lateralis; LP*, *n. lateralis posterior; CM*, *n. centromedian; LG*, *n. geniculatus lateralis.* Numbers indicate serial position of section.

Table 3 presents the delayed-alternation data (Phase III). Of the eight animals studied, only C1 achieved criterion. The ventromedial operates and C3 attained a level of performance significantly better than chance but below criterion. No dorsolateral operate, however, ever performed reliably better than chance.

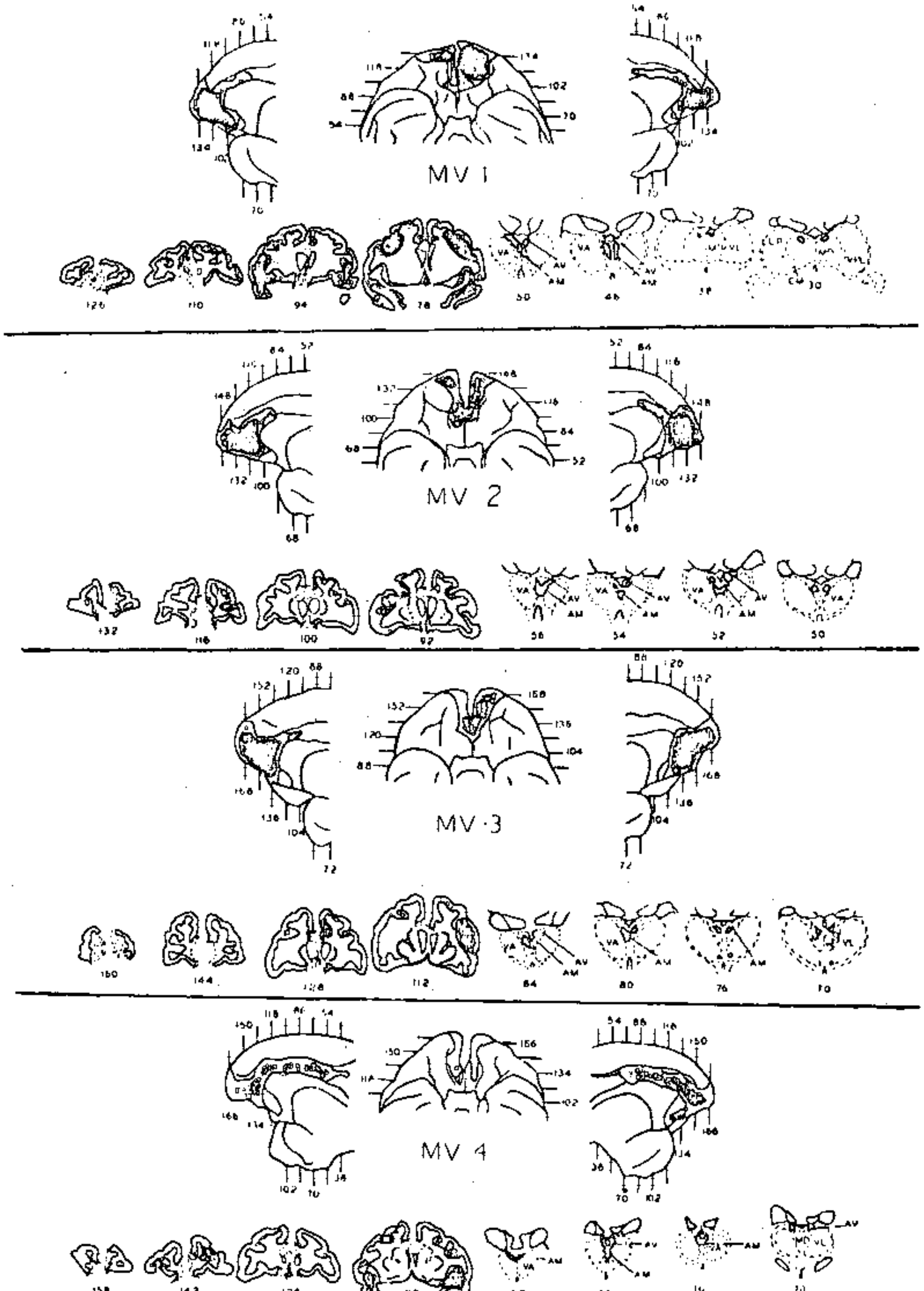

FIG. 2. MEDIAL AND VENTRAL RECONSTRUCTIONS OF VENTROMEDIAL LESIONS
See Fig. 1 for nomenclature.

Comparison of the records of the animals' general behavior in the testing situation revealed few changes after surgery. Thus, there was no clear indication in any animal of a postoperative alteration in kind and degree of reactivity or of vocalization. However, instances of hypermotility were observed in the dorsolateral operates more frequently after operation than before.

In accord with the foregoing observation are the quantitative data obtained postoperatively on those animals that were placed in the activity cage. The average hourly count for the dorsolateral operates ranged from 1,700 to 1,850 as compared with a range of 700 to 1,000 for four of the other five animals studied. VM2, which fell outside this range, attained an average hourly count of 2,400, but this animal was judged to be extremely active preoperatively, and no increase was observed postoperatively.

Anatomical Results

Figures 1 and 2 present the histological findings. The dorsolateral lesions invade the white matter lying between the *sulci principalis* and *callosomarginalis* and extend caudally above the superior limb of the arcuate sulcus. The ventromedial lesions do not include the caudal end of the subcallosal gyrus, and in the cases of VM1 and VM4 extend far caudally on the anterior cingulate gyrus. Except for these variations, the lesions, as determined by serial analysis and reconstruction, correspond to the intended locus and extent of surgical removal. Further, they show bilateral symmetry and have clean, sharp boundaries.

All animals with lesions of the dorsolateral frontal cortex have massive degeneration of the lateral half of the *n. medialis dorsalis*, a finding which is consistent with those of Walker (20), Mettler (10), and Pribram, Chow, and Semmes (14). The dorsolateral operates also had some degeneration of the *n. ventralis anterior* due, perhaps, to extensive involvement of the cortex medial and caudal to the superior limb of the arcuate sulcus (20). With the exception of minimal degeneration in the dorsocentral part of *n. medialis dorsalis* in VM1 and VM3, none of the animals with ventromedial lesions have degeneration in these thalamic loci. On the other hand, degeneration in the anterior nuclear group is found in all the ventromedial operates (and in DL3 where damage to cortex below the *sulcus callosomarginalis* is present). Degeneration of *n. anterior medialis* has been related to lesions of the precallosal medial frontal cortex in cats by Rose and Woolsey (18) and in monkeys by Mettler (10), and this relationship is confirmed in the present study. Degeneration in the *n. anterior ventralis*, however, is found in only some of these animals, and may be due to interruption of fibers terminating in the posterior cingulate gyrus, an explanation offered by Rose and Woolsey (18) for similar findings in cats. Degeneration in dorsocentral part of the *n. medialis dorsalis*, the area of overlap in the thalamic degeneration of the two groups of animals, has been attributed by Pribram, Chow, and Semmes (14) to involvement of the dorsal portion of monkeys' frontal poles.

DISCUSSION

Frontal lobe resections made in consonance with neuronographically determined subdivisions produced differential behavioral results. All animals with dorsolateral lesions consistently failed the delayed-response–type problems, whether tested for initial learning, retention, or relearning. They took a comparatively large number of trials to perform at criterion on the visual-discrimination problem. In addition, they showed locomotor hyperactivity in a variety of situations. In contrast to these changes, observed consistently in the dorsolateral operates, only two of the four animals with ventromedial lesions showed any alterations. These two animals failed the delayed-response retention test, but both relearned quickly. All three ventromedial operates which were trained on delayed alternation performed at a level well above chance and as high as that achieved by one of the two tested controls (C3).

Although the dorsolateral lesions produced greater alterations in all functions tested, interference with visual-discrimination performance was minimal, confirming the results of previous studies (3, 11, 12, 17) and emphasizing the specificity of the effect of frontal lobe damage on performance on delayed-response–type tests. The additional finding of locomotor hyperactivity following resection of dorsolateral frontal cortex confirms the results of Mettler (9) and others (7, 16). However, this effect is not specific inasmuch as hyperactivity has been produced by orbital and caudate damage as well. (No caudate damage is apparent in the present series of animals.) Furthermore, a dissociation between deficient delayed-response performance and locomotor hyperactivity has repeatedly been established (8, 12, 19).

Since the behavioral differences between the two groups were produced by damage to *adjacent* regions of the frontal lobes, the results permit a more precise description than has been possible heretofore of the anatomical limits of the neuroanatomical-behavioral relationship. The validity of this relationship depends, however, on ascertaining whether an equal mass of cortex was involved in the operations performed on the two groups. Present techniques do not permit accurate assessment of extent of removal, but gross inspection suggests that the dorsolateral lesions are somewhat more extensive and somewhat deeper than the ventromedial lesions. Nevertheless, that the difference in behavior of the two groups is not attributable to differences in extent of lesions is suggested by the findings that (*a*) within each operate group in the present study there does not seem to be any correlation between extent of removal and degree of behavioral deficit; e.g., the two ventromedial operates that had transient deficits do not appear to have had greater involvement of frontal cortex than the other animals of their group; and (*b*) large lesions elsewhere in the cortex (1, 17), or even including some frontal cortex (13), do not seriously interfere with delayed-response–type functions.

Support for the hypothesis that interference with separate neural systems is responsible for the differential behavioral results comes from the histological studies. The cortical damage in the two operate groups resulted in easily distinguishable loci of retrograde degeneration in the thalamus; e.g., the dorsolateral resections produced massive degeneration in the lateral half of the *n. medialis dorsalis*, whereas the ventromedial extirpations resulted in minimal or no degeneration in this nucleus. Inasmuch as different behavioral and histological results were produced by the two lesions, it is suggested that neuronographic data, having guided the removals, are relevant to the problem of cerebral specialization.

SUMMARY

1. Three guinea baboons received resection of dorsolateral frontal cortex, three of ventromedial frontal cortex, and three served as controls. One of the controls subsequently received a ventromedial operation. Lesions were made in consonance with neuronographically determined subdivisions.

2. Preoperatively the animals were trained on delayed-response and visual-discrimination tasks. Postoperatively these tests were again presented, a delayed-alternation problem was administered, and quantitative estimates of locomotor activity were obtained. Throughout the experimental period systematic observations were made of the animals' general behavior.

3. Upon completion of the behavioral observations the animals were sacrificed, their brains sectioned, the lesions reconstructed, and thalamic degeneration determined.

4. Markedly greater alterations in performance on delayed-response–type tests were produced by dorsolateral resections than by ventromedial resections. In addition, the dorsolateral operates showed greater changes in locomotor activity and in retention of the visual-discrimination habit. Correlations were apparent between the locus of lesion and the locus of retrograde degeneration in the thalamus.

5. These differential findings suggest that neuronographic data are relevant to the problem of cerebral specialization.

6. The results support the hypothesis that the integrity of a restricted area of frontal cortex is especially important for performance on delayed-response–type tests. The data indicate that such an area lies in the dorsolateral frontal region anterior to the precentral "motor" cortex.

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