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THE BEHAVIOR OF CHRONIC CATS WITH LESIONS IN THE FRONTAL ASSOCIATION CORTEX

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Abstract. Cats with lesions in the proreal and anterior sigmoid gyri and substantial but subtotal degeneration in the mediodorsal thalamic nucleus were studied for 6 years post-operatively. The control group consisted of normal cats matched for age and previous experience. The results reported here and in Warren's previous progress report indicate that frontal cortical lesions result in several behavioral changes in cats which are like those seen in rhesus monkeys after frontal ablations: impairments in discrimination reversal, double alternation and active avoidance learning, retardation in the rate of habituation to novel neutral stimuli, and a decrease in aggression in competitive social situations. Cats with larger frontal lesions made more errors in reversal learning than cats with smaller lesions.

Frontal cats, unlike frontal rhesus monkeys, are not hyperactive post-operatively and retain some capacity for learning delayed response in the WGTA. It is impossible at present to tell whether these discrepancies reflect species differences in the organization of the frontal lobe system or whether the frontal cortex spared in this series of cats is sufficient to mediate delayed response and to prevent the occurrence of hyperactivity.

Warren et al. (1962) found that cats with lesions in the cortical projection field of the mediodorsal thalamic nucleus (MD) were not impaired in learning delayed response in the Wisconsin General Test Apparatus (WGTA). Since much of the cortex known to receive projections from MD (Rose and Woolsey 1948, Akert 1964) was spared in these animals, a second series of cats including cases with larger frontal ablations was prepared. Although these subjects were only marginally impaired in learning delayed response in the WGTA, they showed a deficit in spatial reversal learning more than three years post-operatively (Warren 1964). This paper reports the results of additional behavior tests and presents the histological findings for this series of frontal cats. We are now confident that the largely negative results obtained in this research do not underestimate the effects of large but subtotal frontal decortications on the behavior of cats.

METHOD

Subjects. Nineteen mongrel cats, 9 frontals and 10 unoperated controls, were studied. All received extensive pre-operative training on several learning tasks (Warren 1964), and the frontal and control groups were matched for pre-operative performance in discrimination learning.

Six frontals and six controls survived to complete 27 post-operative experiments. The experiments which have not previously been reported (Warren 1964, Warren and Warren 1966) are listed in chronological sequence in Table I.

TABLE I
Sequence of behavioral tests

Experiment	Median post-operative months
18. Activity — Cage	50
19. Activity — Open field	54
20. Activity — Wheel	56
21 and 22. Spatial reversal learning	57
23. Visual reversal learning	64
24. Deprivation and activity	65
25. Exploration	68
26. Passive avoidance learning	70
27. Active avoidance learning	72

Surgery. The cat, under sodium pentobarbital anesthesia (40 mg/kg) was fixed in a head holder and the scalp incised in the midline. Trephine holes in the bone over the frontal sinus were enlarged with rongeurs to remove the roof and posterior wall of the sinus. The dura was cut and retracted, while the lesion was made by subpial aspiration. The dural edges were then closed with ophthalmic suture, the sinus packed with gelfoam and the wound closed in anatomic layers. All lesions were made under aseptic conditions.

ANATOMY

Methods. The frontal cats were perfused with normal saline followed by 10% formalin in saline at sacrifice, or as soon as possible after death from disease. The brains were fixed in formalin, photographed, dehydrated, embedded in celloidin and cut in 30 micron sections; the brain of one cat (65) was cut in 50 micron sections. Every fifth section was stained with thionine and mounted.

Results. Reconstructions of the cortical lesions in 6 frontal preparations are shown in Fig. 1, and representative sections through the cortical lesions and the thalami for the remaining three cats, those with the smallest, median and largest cortical lesions are presented in Fig. 2, 3 and 4 respectively. The stippled cortical areas in these Figures represent regions which were severely undercut.

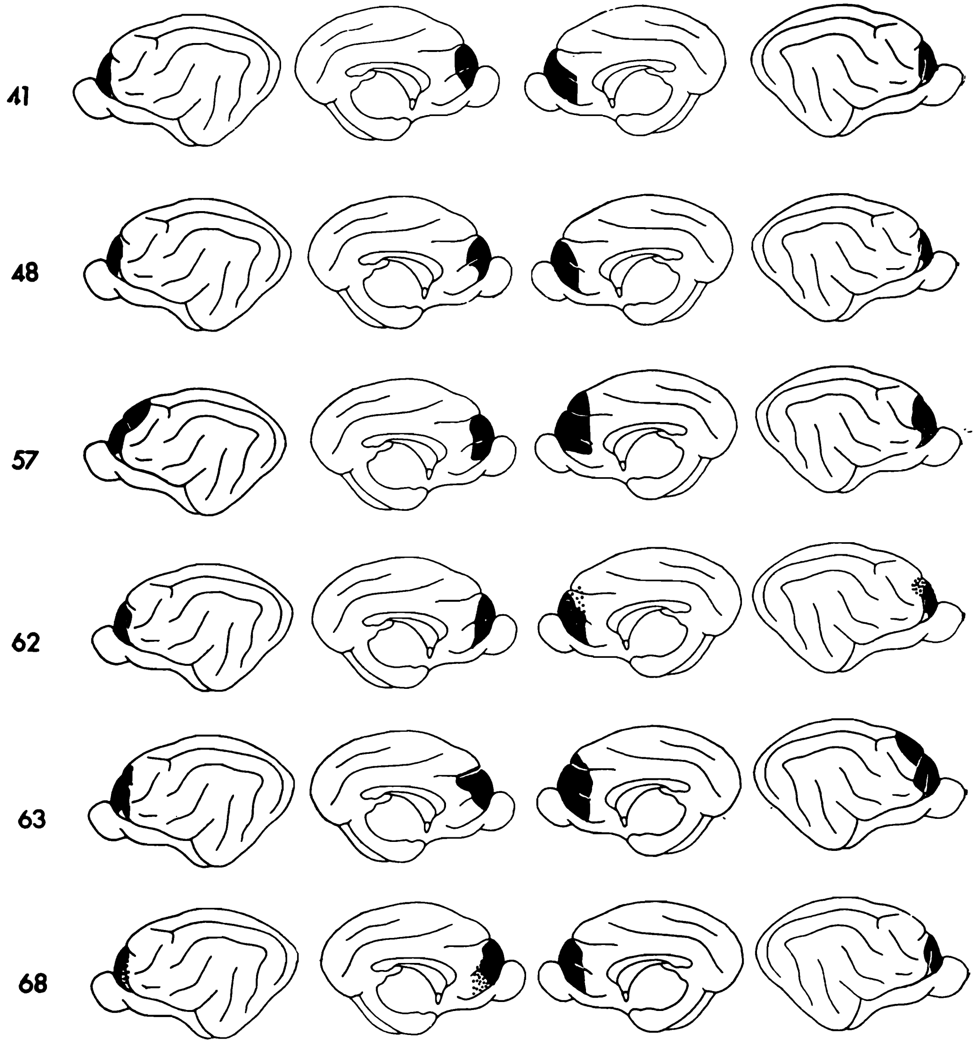

Fig. 1. Reconstructions of the cortical lesions.

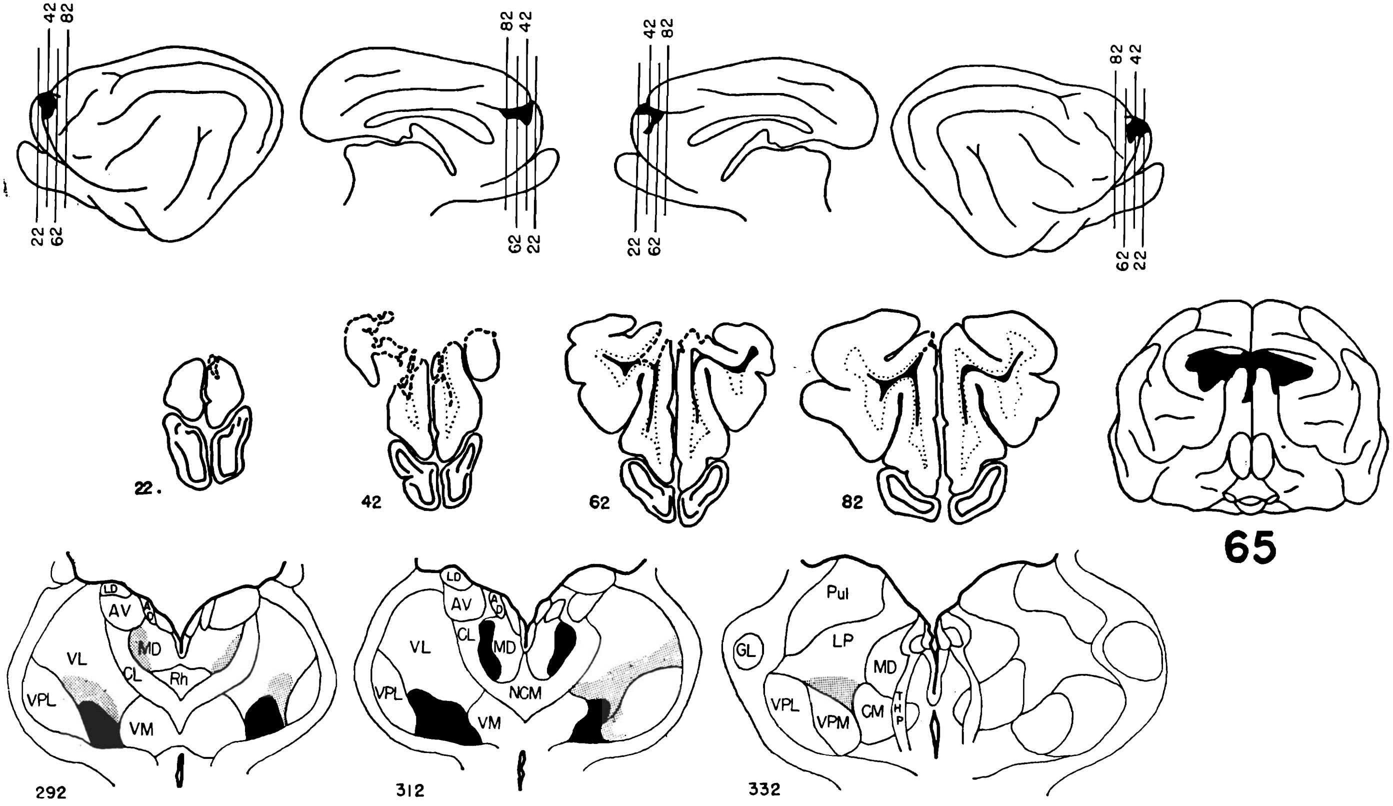

Fig. 2. Cortical damage and retrograde degeneration in the cat with the smallest frontal lesion.

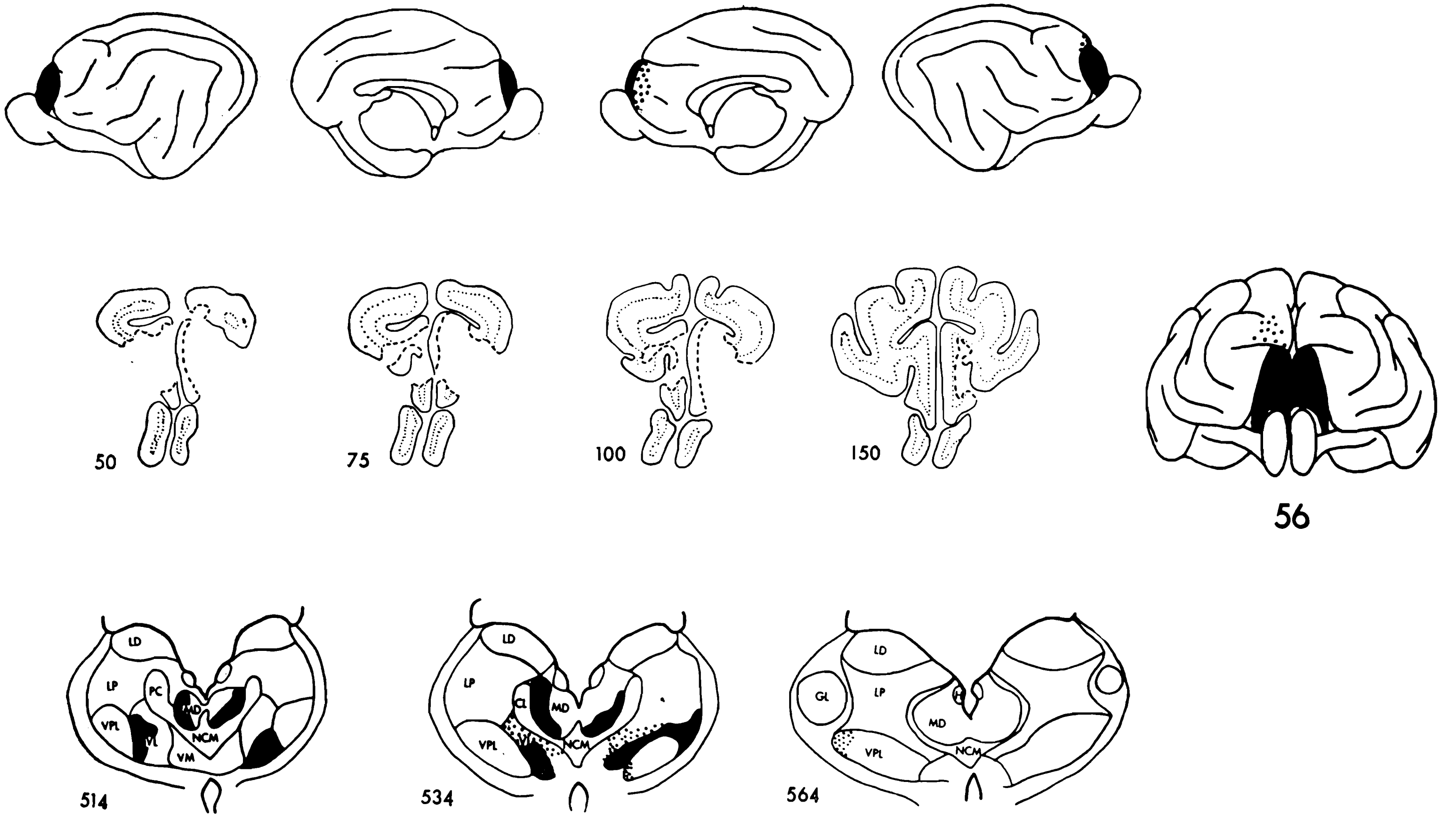

Fig. 3. Cortical damage and retrograde degeneration in the cat with median frontal lesion.

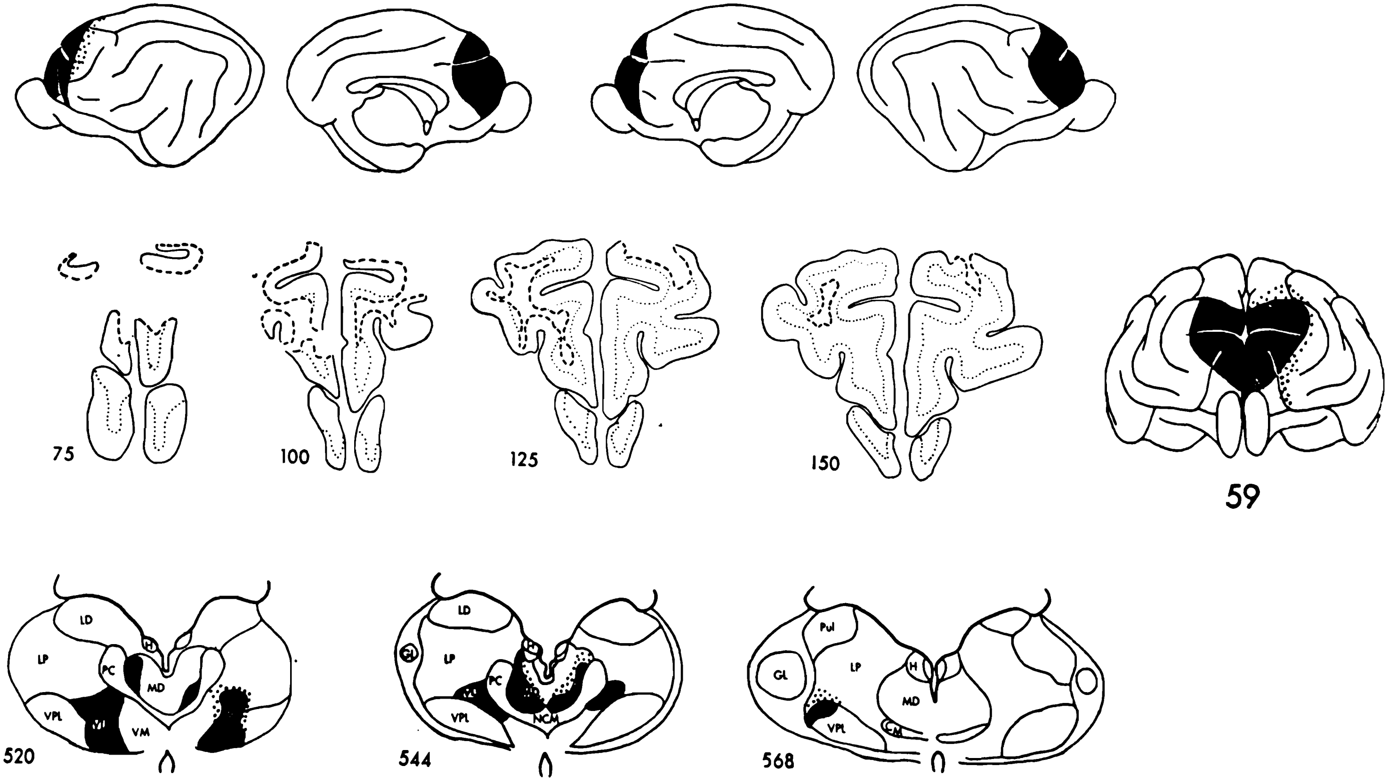

Fig. 4. Cortical damage and retrograde degeneration in the cat with the largest cortical lesion.

In general, the cats in this series incurred substantial but subtotal destruction of the medial and lateral surfaces of gyrus proreus, of the cortex within the presylvian sulcus, and of the anterior sigmoid gyrus. The posterior sigmoid cortex was damaged in three cases. Table II indicates the relative ratings of the individual cats with respect to the extent of cortical destruction and the intensity of retrograde degeneration in the affected thalamic nuclei.

TABLE II

Summary of anatomic findings

Cat	Extent of cortical removal						Thalamic degeneration		
	Completed experiment	Medial proreus	Lateral proreus	Presylvian sulcus	Anterior sigmoid	Posterior sigmoid	MD	VL	VB
41	28	2	2	1	1	0	1	0	0
48	28	2	2	1	1	0	thalamus lost		
56	28	1	2	2	2	0	1	2	0
57	28	3	3	2	3	3	3	2	2
59	28	2	2	0	3	3	3	3	2
62	17	2	2	2	2	0	thalamus lost		
63	17	2	2	2	3	2	thalamus lost		
65	5	1	1	0	3	0	2	3	1
68	28	2	2	1	2	0	1	1	0

Key to ratings. Extent of decortication: 0, none; 1, minimal; 2, small; 3, moderate. Severity of thalamic degeneration: 0, none; 1, just detectable; 2, mild; 3, moderate.

Frontal cats 62, 63 and 65 died before the tests reported in this paper; their histology is given here to document the findings that have already been published on this group (Warren 1964). A consideration of the relation between lesion size and the behavioral results is deferred until after the experimental observations are described.

REVERSAL LEARNING

The frontal cats in Warren et al. (1962) experiment were impaired when required to learn three reversals of a spatial discrimination in a single session in early post-operative tests, but subsequently regained the ability to learn such reversals as well as normal cats. The present group of frontals was impaired on this task even 3 years post-operatively. The experiments described in this section were carried out about 5 years post-operatively and were intended to determine whether the current frontals were permanently retarded in reversal learning, or whether they, too, would eventually recover the ability to learn reversal problems as rapidly as intact cats.

The conditions under which cats are trained on discrimination reversal problems in the WGTA have been described in detail in previous papers (Warren et al. 1962, Warren 1964). The cats were tested under 22–23 hr of food deprivation and were rewarded for correct responses with pieces of pork kidney.

Experiment 21. Reversal learning with combined spatial and visual cues

The stimuli were a small thick white rectangle which was always presented on the left, and a large thin black T, always presented on the right side of a grey test tray in the WGTA. The cats were trained to respond consistently to the right or left until they made 11 correct responses in 12 non-correction trials, with the last 8 responses all correct. At this time the opposite side became correct. The subjects were trained on three such reversals per day for 10 days.

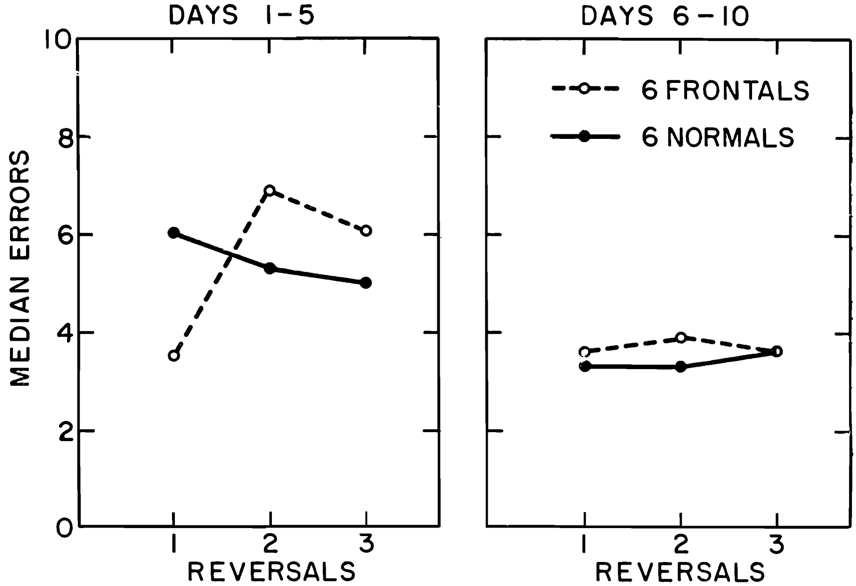

Fig. 5. Errors to criterion on reversals with combined visual and spatial cues.

Median errors to criterion are plotted as a function of reversals within sessions over days 1 through 5 and days 6 through 10 in the panels of Fig. 5. None of the differences between the frontal and control groups approaches statistical significance. The performance of the operated and normal cats is almost identical in the last half of the experiment. This finding indicates that prolonged retraining and/or extended recovery time results in the eventual disappearance of the spatial reversal learning deficit which was conspicuous in earlier tests with this group and in other series of frontal cats (Warren et al. 1962, 1969).

Experiment 22. Spatial reversal learning with irrelevant visual cues

This experiment was undertaken to ascertain whether the frontals would be impaired on a potentially more difficult spatial reversal learning task. The conditions of training were the same as in Experiment 21, except that the position of the white and black objects was varied from side to side in a balanced irregular sequence. The variation in the position of the visual cues was irrelevant to solution of the reversal problems. Spatial cues remained relevant and were consistently rewarded or nonrewarded throughout. The cats' performance on the spatial reversals might have been depressed therefore to the extent that they responded to visual in preference to spatial cues.

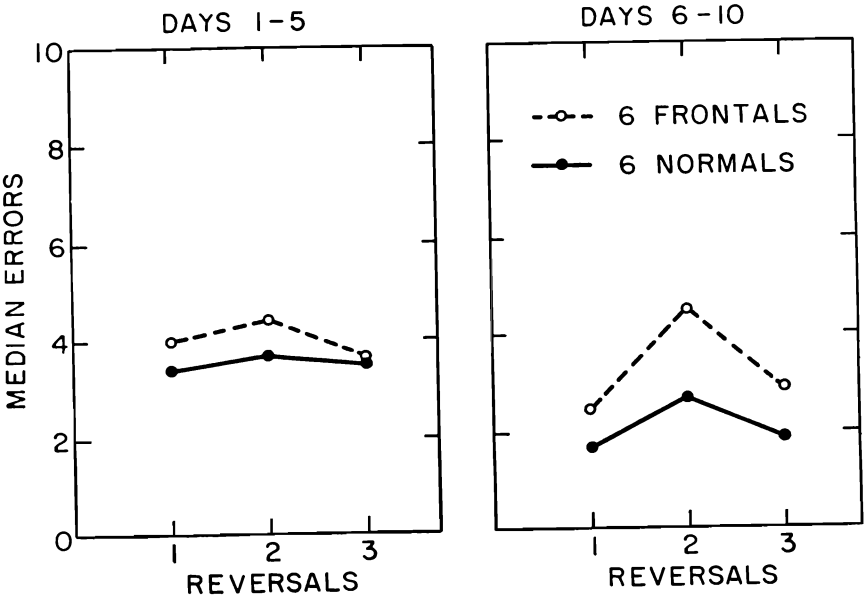

Fig. 6. Errors to criterion on spatial reversals with irrelevant visual cues.

The results are displayed in Fig. 6. Although the frontals made slightly more errors than the normal controls, the groups did not differ significantly in any aspect of their performance. Both groups made approximately the same number of errors as they had in the preceding experiment, indicating that the frontals were no more distracted by irrelevant visual cues than the controls.

Experiment 23. Visual reversal learning

The frontal cats had obviously regained the ability to learn spatial reversal problems when tested with recurrent familiar objects and under conditions of massed testing. This experiment was designed to investigate whether these conditions would produce a deficit in learning serial reversals of a more difficult object discrimination task, with visual cues relevant and spatial cues irrelevant.

The discriminanda were a large thick grey triangle and a small thin white quadrilateral. The subjects were trained to a criterion of 10 consecutive correct responses in a single session on 60 consecutive reversals of this discrimination. The cats were given a maximum of 50 noncorrection trials in a single test session, and training for the day was discontinued immediately when an animal satisfied the criterion. In this experiment the reward value of the stimuli was always reversed between sessions and never within sessions.

The results are presented in Fig. 7 and 8. Figure 7 shows the median

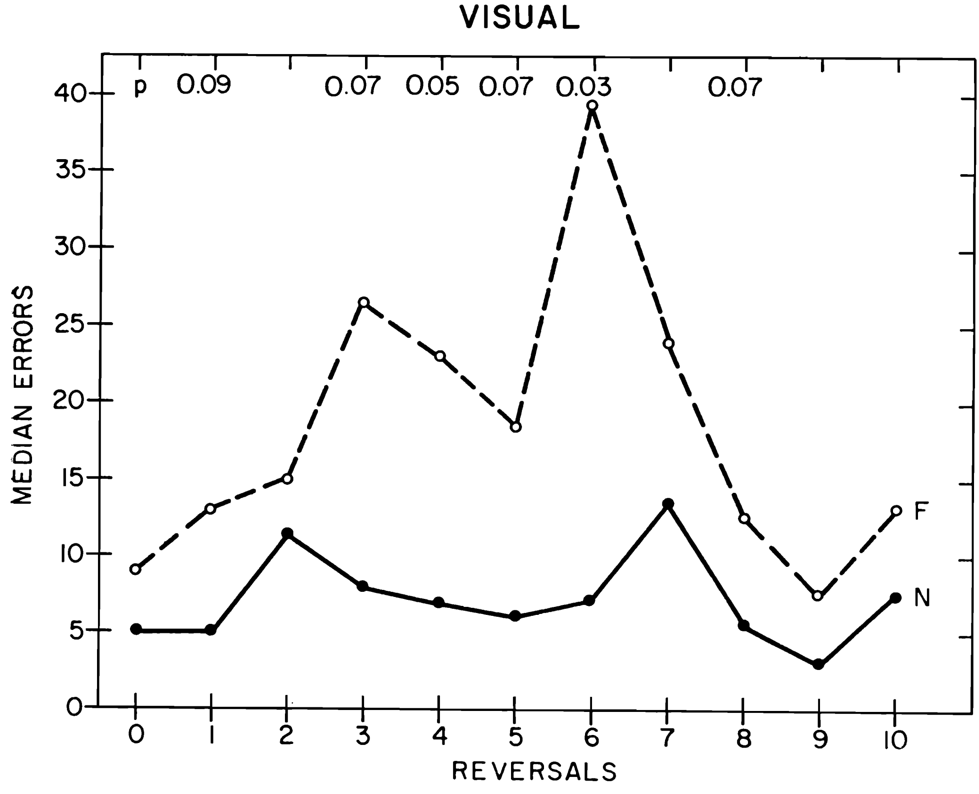

Fig. 7. Errors to criterion on visual discrimination and 10 reversal problems.

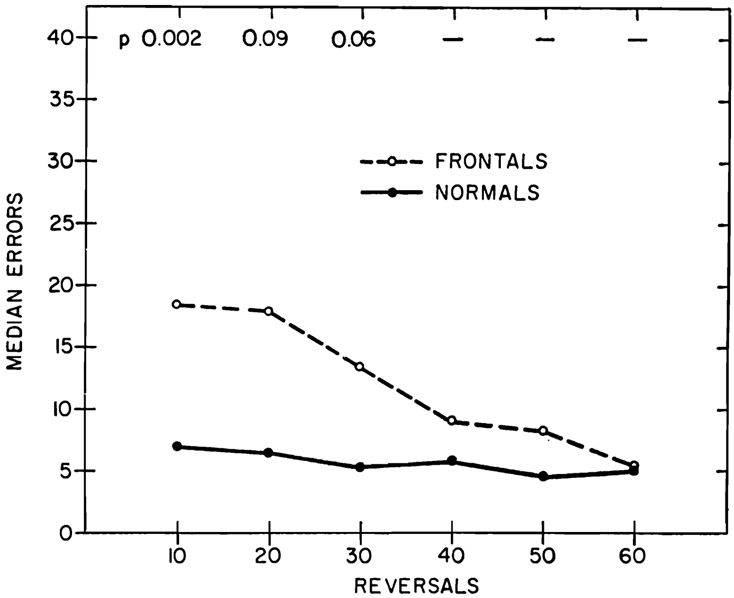

Fig. 8. Errors to criterion on successive blocks of 10 visual discrimination reversals

number of errors to criterion for the normal and frontal cats on the initial discrimination (Reversal 0) and each of the first 10 reversals; the probability that the intergroup difference on each reversal is significantly different from chance is indicated at the top of the Figure when $p < 0.10$. It will be noted that the groups did not differ appreciably in performance in original learning nor on the first two reversals, and that the disparity between the groups increases markedly from reversals 3 through 6. This pattern tends strongly to confirm the interpretation (Warren 1964) that cumulative proactive interference effects are important in the production of a reversal learning deficit in frontal cats.

The median number of errors on successive blocks of 10 reversals each is given in Fig. 8, which shows that the impairment observed in the frontal cats tends progressively to diminish with extended training on this task so that the frontals' scores on the last 10 reversals closely approximate those of the controls.

Discussion. Cats with lesions in the frontal association cortex are impaired in learning object and spatial reversals but can, given prolonged post-operative training, regain normal levels of proficiency on such tasks. These findings are clearly consonant with those obtained by Warren, Warren and Akert (1962).

Rhesus monkeys with lesions in the orbital frontal cortex are also impaired on serial reversals of either spatial or visual discrimination problems (Mishkin 1964, Butter 1969, Goldman et al. 1970, Iversen and Mishkin 1970). The effects of extended post-operative training on reversal learning by rhesus monkeys with orbital lesions are unknown so no comparisons may be made concerning the duration of this defect in cats and rhesus macaques. Divac (1971) has shown, however, that the impairment of spatial reversal learning in rats with lesions in the cortical projection of MD is much less persistent than that seen in cats.

AVOIDANCE LEARNING

Rhesus monkey with lesions in the frontal granular cortex are impaired in performance on active avoidance tasks (Smith et al. 1956, Pribram and Weiskrantz 1957, Waterhouse 1957). Cats with very large cortical and subcortical lesions that include the proreal and orbital gyri are also deficient in retention of active avoidance responses (Brady et al. 1954). These observations suggest that cats with ablations of the frontal association cortex might be deficient in learning active avoidance responses.

McCleary's (1961) demonstration that cats with lesions in the septal inhibitory zone are impaired in learning passive but not active avoidance responses suggested an alternative hypothesis. Cats with ablations of the frontal inhibitory cortex might also be impaired in passive avoidance learning and unaffected in active avoidance learning. Our frontal cats were tested on both active and passive avoidance tasks to determine whether frontal lesions produced effects like those seen in frontal monkeys or in septal cats.

Experiment 26. Passive avoidance

The apparatus was a box, 48 cm high, 58 cm wide and 43 cm deep, with a grid floor and a glass front wall that extended to 5 cm above the floor. A metal shelf, 11 cm wide, was attached to the front of the box and the cats were able to secure small pieces of meat on the shelf by reaching under the glass. An opaque screen was raised and lowered by the experimenter to start and to end discrete-trial presentations of the food. The cats were adapted by allowing them to take 10 pieces of meat without punishment. None of the animals failed to take the meat within 1 min on the adaptation trials.

Five 1-min trials were given each day in passive avoidance training. The cats were shocked each time they touched the meat with their paws or mouth; the intensity of the shock was adjusted to be just sufficient to prevent contacts with the food, and varied between 2.0 and 3.5 ma for individual subjects. The animals were trained under 23 hr of food deprivation, to a criterion of 15 consecutive trials without touching the meat. Upon attaining criterion, each cat was placed on total deprivation of food and tested five trials a day, without shock, to an extinction criterion of three consecutive responses with latencies of less than 1 min, or for a maximum of 10 days.

Sometimes the cats made more than one attempt to take the meat during a single trial, so learning performance is described in terms of two dependent variables: trials and total shocks to criterion. Table III gives the level of shock required to prevent responding by each cat, shocks and trials to criterion in learning, and trials to criterion in extinction. The frontals were as sensitive to shock as the controls, learned the passive avoidance response with fewer trials and shocks, and extinguished the passive avoidance response somewhat more quickly than the unoperated controls. None of the intergroup differences was significant. The experiment thus yields no evidence of a significant impairment in passive avoidance by cats with lesions in the frontal association cortex.

TABLE III

Passive avoidance learning by frontal and normal cats

Cat	Shock intensity (in milliamperes)	Learning trials	Learning shocks	Extinction trials
41	3.0	35	7	24
48	3.0	1	3	7
56	3.0	4	5	1
57	2.0	21	4	30
59	3.0	2	2	0
68	3.0	1	2	5
Frontal median	3.0	3	3.5	6
42	3.0	88	21	18
61	3.0	21	9	9
64	3.5	66	23	0
66	3.0	8	5	19
79	2.0	7	3	50
82	2.0	23	9	0
Control median	3.0	22	9	13.5

Discussion. Cornwell (1966) tested cats on passive avoidance under essentially the same conditions as McCleary's (1961) septal preparation, and found no significant difference between animals with lesions in gyrus proreus and controls. Frontal cats in Warren et al. (1962) series learned passive avoidance as quickly as unoperated subjects. Consistent failures to demonstrate a defect in simple passive avoidance learning by frontal cats indicate that the frontal cortex does not mediate the same sort of inhibition as the septal area does in respect to learning passive avoidance.

Experiment 27. Active avoidance learning

The two-compartment shuttle box used in this experiment has been described in detail by Wilson et al. (1965). Each trial began when the experimenter raised the door between the compartments. Elevation of the door activated a buzzer and started a Hunter interval timer. The cat could avoid shock by crossing into the opposite compartment within 5 sec after onset of the buzzer. If the subject failed to respond in 5 sec, a 3.0 ma shock came on and continued for 2 min unless the animal made an escape response.

The cats were tested 5 trials a day to a criterion of 9 avoidance responses in 10 trials (2 consecutive sessions). Cats that failed to learn in 200 trials were given an additional 100 trials under massed training conditions, 20 trials per day for 5 days. Animals that met the acquisition criterion were next extinguished, under no-shock conditions, to a criterion of no more than 1 response in 10 successive trials, then retrained to the same criterion and under the same conditions as in original learning. In the final stage of the experiment, the subjects were extinguished by counterconditioning, i.e. they were shocked whenever they crossed the barrier to the other compartment after presentation of the conditioned stimulus.

The results are summarized in Table IV where an *F* preceding a learning score indicates failure to learn within 300 trials. The frontal group was significantly inferior to the controls in initial learning ($U = 6$, $p = 0.032$). The three frontals which failed to learn to make active avoidance responses made prompt escape responses throughout training. It is unlikely that their performance defect reflected any serious motor disability or insensitivity to shock (*see* Tables III and IV). None of the differences between the frontals that learned the avoidance response and the controls on the extinction, relearning and counterconditioning tests was significant.

Discussion. The effects of frontal lesions upon active avoidance by cats vary as a function of the particular task and of the performance measure, acquisition or retention, used in a given experiment. Cats with lesions in gyrus proreus are not impaired in learning a simple and unambiguous one-way avoidance response (Cornwell 1966). The present experiment and that of Axelrod and Diamond (1955) show, however, that

TABLE IV

Active avoidance learning by frontal and normal cats

Cat	Learning	Extinction	Relearning	Counter-conditioning
41	37	122	11	13
48	128	11	141	17
56	85	5	6	11
57	*F*300	—	—	—
59	*F*300	—	—	—
68	*F*300	—	—	—
Frontal median	214	11	11	13
42	32	98	7	18
61	57	85	5	3
64	95	25	25	25
66	45	6	5	1
79	59	59	6	1
82	70	22	5	3
Control median	58	42	5.5	3.0

cats with frontal injuries are retarded in initial acquisition of active avoidance when trained in a two-way avoidance apparatus where both compartments are occasionally associated with shock.

L. W. Coutant and J. M. Warren (unpublished data) trained ten cats on passive and two-way active avoidance under conditions identical with those of Experiments 26 and 27. Five animals were then subjected to ablations of gyrus proreus like those of cases 56 and 68, and their postoperative retention was compared with the relearning scores of five unoperated controls, with the results shown in Table V. The frontals retained both tasks quite well and were not significantly different from the controls on either task. These findings indicate that frontal lesions which interfere with the original learning of active avoidance in a two compartment shuttle box have no effect on the retention of such habits.

Nielson and Davis (1966) have also shown that destruction of the proreal, anterior sigmoid and posterior sigmoid gyri have no effect on the retention of leg flexion avoidance responses to acoustic stimuli in cats. On the other hand, Zieliński et al. (1962) and Zieliński (1966) found that proreus lesions produced a significant but transient impairment in the retention of a bar-press avoidance response by cats.

Two general conclusions may be advanced concerning the effects of frontal lesions on avoidance learning by cats. It is clear that frontal lesions do not produce effects like those resulting from septal lesions in cats, since frontal cats, unlike septal cats, are not impaired on passive

TABLE V

Trials to criterion on active and passive avoidance

	Active		Passive	
	Pre-op.	Post-op.	Pre-op.	Post-op.
Controls				
63-10	12	0	10	0
247	13	0	10	0
245	27	27	5	0
229	80	6	10	10
196	39	2	15	0
Median	27	2	10	0
Frontals				
63-47	18	16	15	0
230	12	12	5	0
197	21	0	5	0
198	60	15	15	5
228	26	4	15	0
Median	21	12	15	0

avoidance and are deficient in learning two-way active avoidance responses. The evidence also suggests that frontal ablations may have more severe effects on active avoidance performance in rhesus monkeys than in cats. Frontal lesions impair the acquisition but not the retention of two-way avoidance responses in cats while rhesus monkeys show deficits in both the acquisition (Smith et al. 1956) and retention (Pribram and Weiskrantz 1957) of active avoidance responses when tested in a two-compartment shuttle box.

ACTIVITY

Rhesus monkeys with lesions in the frontal granular cortex are generally much more active than normal monkeys (French 1959, Gross and Weiskrantz 1964). Although Langworthy and Richter (1939) and Smith (1942) reported that cats with unverified frontal lesions were hyperactive post-operatively, neither Konorski and Lawicka (1964) nor Warren et al. (1962) observed any conspicuous increase in activity in cats with lesions involving primarily gyrus proreus. An extensive series of activity tests were carried out with the present series of cats to determine more precisely the effects of frontal lesions upon locomotor activity levels in cats. The subjects were observed in three different apparatus, under a variety of stimulus and motivational conditions, since experiments with both rhesus monkeys (Gross and Weiskrantz 1964) and with rats (Lynch 1970) indicate that these variables may strongly affect the activity of normal and brain injured animals.

Experiment 18. Activity in a test cage

The apparatus was a 75 cm cubical cage with two infrared light beams that impinged on photosensitive recording units and divided the cage into four equal quadrants. Each time the cat moved from one quadrant to another the interruption of the light beam was recorded on a digital counter. The number of interruptions was recorded on a separate counter for each of five successive 4-min periods.

The subjects were tested 20 min a day for 40 days. Half the observations were made with the sound shielded testing room illuminated by a 150 w bulb and half with the same room in darkness, the two conditions being alternated in ABBA or BAAB order for subgroups of normals and frontals.

Neither the frontal nor the intact cats' activity was affected by testing in the light and dark. The panel on the left in Fig. 9 shows the median number of beam interruptions for the two groups on successive blocks of 10 days, and the right panel shows the total number of inter-

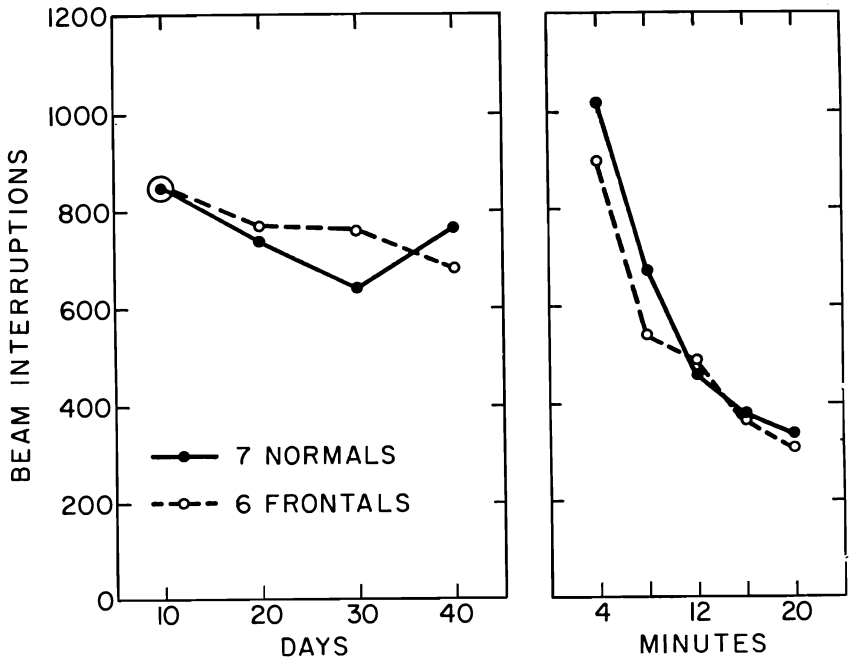

Fig. 9. Median inter- and intra-session activity functions in the activity cage.

ruptions during successive 4-min periods, summed over days. The performance of the frontal animals, both between and within days, is almost identical with that of the normal cats, and none of the differences between the groups approached statistical significance.

Experiment 19. Activity in an open field

The cats were released from a large enclosed starting box and allowed to move freely about a 3.6 by 3.6 m enclosure for 5 min in each of 30 test sessions. The animals' activity score was the total number of 60 cm squares entered during each test period. None of the subjects had been in the test area prior to this study.

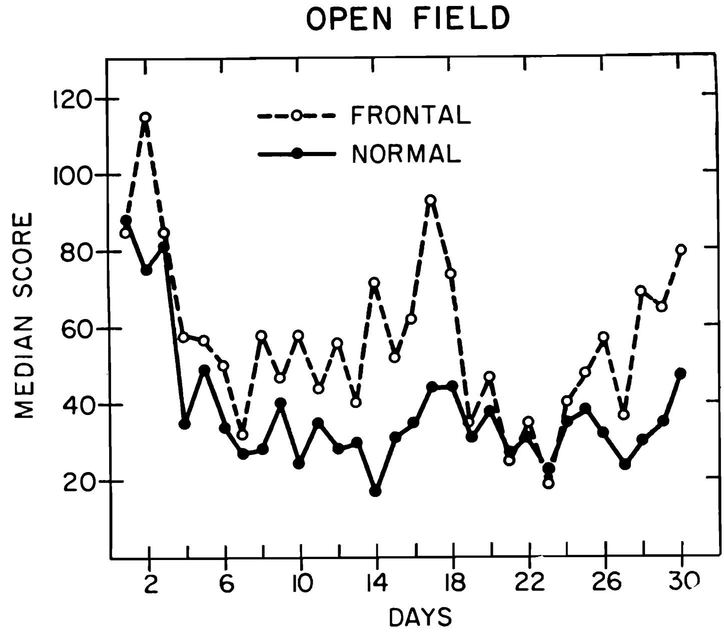

Fig. 10. Median activity scores in the open field.

The results of the experiment are summarized in Fig. 10 and Table VI. Both the frontal and control cats were quite active on the first 3 days in the novel testing situation. The curve for the normal animals is at a low, relatively constant, level from day 4 through 30, suggesting that the intact subjects habituated rather quickly in this unfamiliar environment. The frontal animals had higher median scores than the controls on 27 of 30 tests, and the curve for the frontal is more variable and does not suggest any consistent reduction in activity with continued testing.

The mean activity scores for individual cats on days 1 through 3 and days 4 through 30 are presented in Table VI, which also shows the percentage of change in activity from the first 3 to the last 27 days of the experiment. It is immediately apparent that the range of individual diffrences within groups is so wide as to preclude any claim that the normal and frontal cats differ in absolute levels of activity, either early or late in the experiment. It will be noted, however, that the normal cats showed a greater reduction in activity from the first to the second period of testing than the frontals ($U = 8$, $p = 0.066$); t-tests for related measures indicate that the normals ($t = 4.23$, $p < 0.01$), but not the frontals ($t = 1.26$), had significantly lower scores on days 4–30 than on days 1–3.

These findings, indicative of an impairment in the habituation of locomotor activity in a novel situation in frontal cats, have been replicated in two subsequent series of cats with lesions largely confined to gyrus proreus.

Experiment 20. Performance in an activity wheel

The apparatus was a Wahmann activity wheel, identical in design to the wheels frequently used in studies with rats, but large enough to accommodate cats comfortably (wheel diameter, 80 cm; wheel width, 18 cm; cage, 30 by 35 by 45 cm).

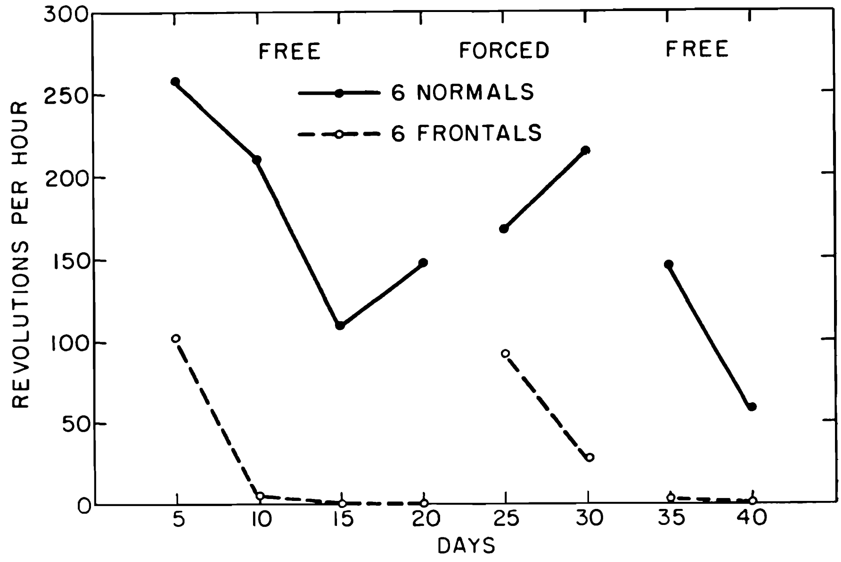

Fig. 11. Median scores in the activity wheel.

Each animal was tested for 40 days. On days 1 through 20 and 31 through 40, the subjects were placed in the cage adjacent to the wheel and removed after 1 hr; during this period the cat was free to enter the wheel or not.

On days 21 through 30, the cats were placed in the wheel and the door to the cage was closed to prevent the animal from leaving the wheel; during this phase of the experiment the subjects remained in the activity wheel overnight, for 12 hr each night.

Median activity scores (revolutions per hour) for the normals and frontal over successive blocks of 5 days are shown in Fig. 11, which shows that the intact controls were more active than frontals throughout the experiment. The variance within groups was, however, so great that the performance of the normal and frontal cats differs significantly only over the period from day 31 to 35 ($U = 5.5$, $p = 0.03$).

Experiment 25. Deprivation and activity

The purpose of this experiment was to determine if cats with frontal ablations differ from unoperated cats in respect to the effect of food deprivation upon activity in the test cage used in Experiment 18. The animals were tested for 12 days. They were observed 12 hr after feeding on days 1 through 5, and days 11 and 12. They were subjected to complete food deprivation from days 6 through 10, and were tested 24, 48, 72, 96 and 120 hours after the last feeding during this period. The cats were allowed to feed ad lib. after the 120 hr test on day 10 and retested 6 hr later, under satiated conditions.

The median weight loss over 5 days without food was 11% (range: 6–24). The frontals and controls did not differ significantly in regard to the percentage of weight loss, and the members of both groups all ate sufficient food to compensate for the loss in weight between the deprived and satiated tests on day 10.

Figure 12 shows the median number of beam interruptions for the normal and frontal groups on successive days of testing. The frontal cats were generally somewhat less active than the controls, and showed a less consistent response to progressively greater degrees of food deprivation. The scores of the control animals were significantly higher than those of the frontals in the test under 120 hr of food deprivation on day 10 ($U = 4$, $p = 0.013$) and also in the test under control conditions on day 11 ($U = 6$, $p = 0.032$) and on day 12 ($U = 6$, $p < 0.032$).

It is clear that food deprivation has less effect upon the behavior of frontal than upon normal cats in the activity cage situation. Absolutely no evidence for the notion that hunger might potentiate hyperactivity

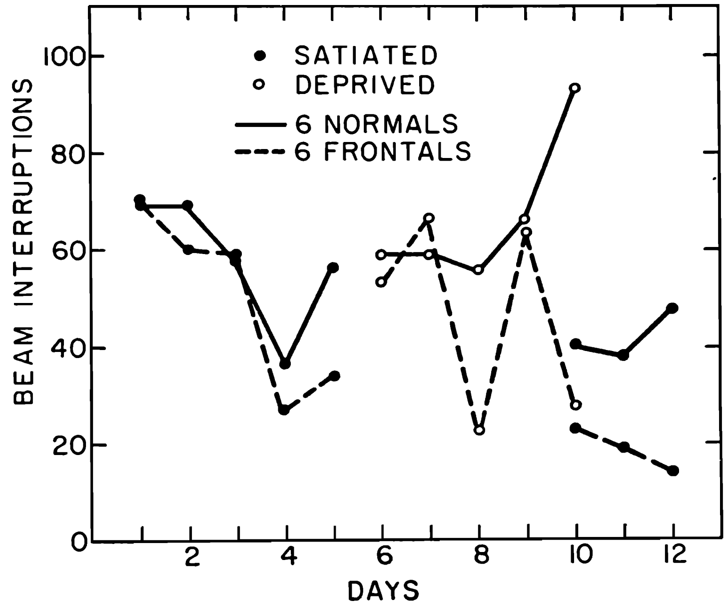

Fig. 12. Effect of food deprivation on activity of cats in the cage situation.

in frontal preparations was obtained in this experiment, which must therefore be regarded as confirming and extending the generality of the negative results of Experiment 18.

Experiment 26. Exploratory behavior

Akert noted that acute cats with extensive lesions in the frontal association cortex (Akert 1964, Fig. 18-17) were extremely active in the presence of novel stimuli and in unfamiliar environments, even though they were not grossly hyperactive in familiar situations.

The purposes of this experiment were to compare the habituation of exploratory activity in normal and frontal cats in an unfamiliar environment, to determine the effect of presenting novel stimuli on locomotor activity in normal and frontal cats, and to assess the effects of food deprivation upon activity in an open field situation.

The cats were observed through a one-way screen in an unfamiliar room, 3 by 4 m, for 5 min a day for 51 days. On 19 of the testing sessions stimuli calculated to evoke investigatory responses from cats were presented in the center of the room according to the schedule given in Table VII. The missing days in the phases listed in Table VII were control days with no novel stimulus in the test room.

The cats were tested 4 hr after their last feeding throughout the

TABLE VI

Mean activity scores in the open field

Cat	Days 1–3	Days 4–30	Change (in percent)
41	55	60	+9
48	41	25	—39
56	99	16	—84
57	169	129	—24
59	125	133	+6
68	88	34	—61
Frontal median	93	47	—31
42	84	37	—54
61	115	50	—57
64	12	2	—83
66	111	40	—64
79	26	4	—85
82	81	43	—47
Control median	82	38	—60

experiment, except that they were deprived of food from days 45 through 49 and were tested under 28, 52, 76, 100 and 124 hr deprivation on these days.

The animals were observed in the empty room without novel stimuli on the remaining days of the experiment. The observer recorded the number of 60 cm squares entered in each test period, and noted the occurrences of piloerection, arching of the back, proximity to, and contact with, the novel test stimuli, and latency to contact the object. The amount of food ingested on the test sessions with unfamiliar foods was also recorded.

The activity scores for the normal and frontal cats are presented in Fig. 13. In general, the performance of the groups is quite similar. Both groups show a rapid decrease in activity over the initial four control sessions, a moderate increase in activity on most days in the series with humans and animals in the test room, followed by a marked decrease in activity on those days when food was available, and an elevation in activity from day 45 through 49 when the animals were tested under total deprivation of food.

Very few response measures showed a significant difference between the normal and frontal cats. The following list is exhaustive. The normal cats had significantly lower activity scores than the frontals on day 9 (human pets when cat approaches) and on day 13 (human holds and pets cat at the start of the session); on both days $U = 7$, $p = 0.047$. The normal cats were also significantly slower to leave the stimulus person

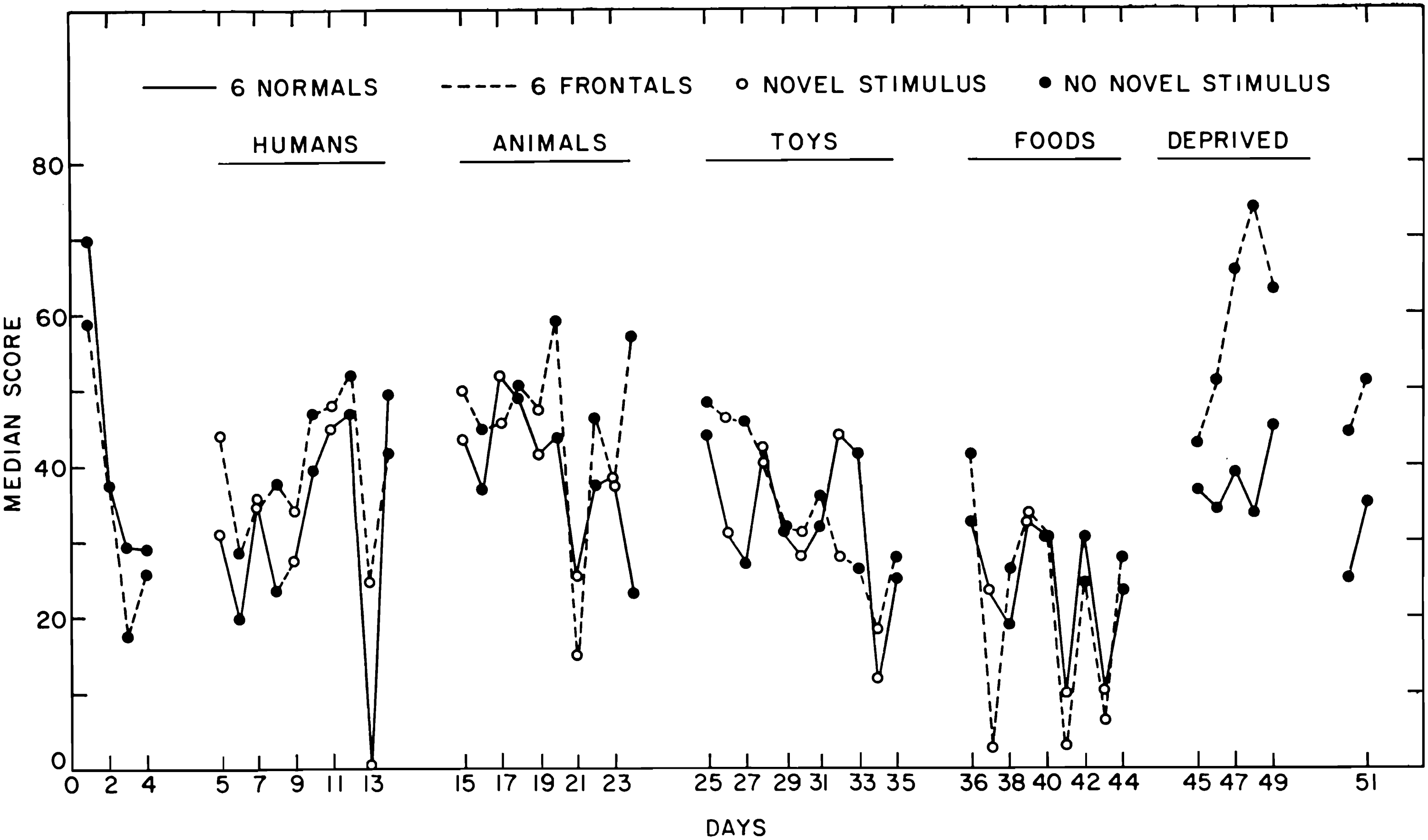

Fig. 13. Median scores on exploration tests in the open field.

on day 13 ($U = 6$, $p = 0.032$). These differences suggest that frontal cats are more indifferent toward humans than normal cats.

The frontal cats were significantly less active than their controls on days 37 (fish roe) and 41 (tuna); they also approached the fish roe (day 37) and the marble and pop beads (day 26) with significantly shorter latencies than the controls, and ate significantly more of the test food on day 39 when pigs feet were presented. These findings are compatible with the idea that frontals may be somewhat more ready to approach novel toys and foods than intact cats. It is clearly impossible to assert that either group is generally more or less fearful than the other since different results were obtained in the tests with humans and strange foods.

Although the frontal group was consistently more active than the controls in the five tests under conditions of food deprivation, none of the intergroup differences approached statistical significance. Thus the results of this experiment demonstrate a high degree of resemblance in the behavior of the frontal and control cats. In contrast to Experiment 19, there was no suggestion that frontal cats differed from the controls in habituation to the testing situation. The results of this experiment cannot, however, be construed as contradicting Experiment 19. Both the operated and intact cats were more active on *both* experimental and control days in the present experiment, indicating that frequent shifts between tests with and without novel stimuli retard habituation to the same extent in normal and frontal cats. There was no convincing indication that chronic frontals are more reactive than normals to changes in external stimulus conditions or to moderate degrees of food deprivation, at least as measured by locomotor activity scores. The findings indicative of aversion to humans and more prompt approach to strange foods by the frontal cats require replication before speculation regarding the significance of these observations is justified.

Discussion. Our activity experiments show that frontal cats are not generally hyperactive. Although the frontals were more active than the controls in the open field situation of Experiment 19, two facts argue against interpreting this as an indication of gross hyperactivity in the frontal preparations. The normal and frontal cats were equally active in the first few test sessions, and the two groups were equally active in the same situation when appropriate incentives for exploration were provided in Experiment 25.

We consequently interpret the positive result of Experiment 19 as a failure of habituation to an initially novel situation by frontal cats, possibly similar to the retardation in extinction of the orientation reflex in cats with frontal lesions noted by Jouvet (1961), and not as an instance of the sort of hyperactivity characteristic of rhesus monkeys. This interpretation implies that the retarded habituation of exploratory behavior seen in our cats is analogous to the slower habituation of responses to salient irrelevant stimuli in learning situations observed in frontal rhesus monkeys (Butter 1964, Grueninger and Pribram 1969).

CORRELATION OF ANATOMIC AND BEHAVIORAL RESULTS

The histological findings, presented in Fig. 1 through 4 and in Table I, indicate that it would be difficult to rank the frontal cases in this series unambiguously in terms of total amount of frontal cortical damage. It does not seem unreasonable, however, to dichotomize the group. Frontal cats 57, 59 and 63 sustained more extensive removals of the cortical projection area of MD (Akert 1964) and manifested more severe degeneration in MD than in the remaining six frontal cases.

The scores for the individual frontals on the learning tasks which yielded a significant difference between the normal and operated cats were examined for evidence of differences between the cats with larger and smaller frontal ablations. The frontals' ranks on five reversal learning tasks, described in this paper or in Warren's (1964) progress report, are given in Table VIII which shows that the cats with more extensive lesions made significantly more errors in the early post-operative tests of spatial reversal learning (Experiments 1 and 2), and that the animals with larger lesions made more errors than any of the subjects with smaller lesions on repeated reversals of a visual discrimination (Experiment 26). The cases with large lesions showed greater overall impairment in reversal learning, as indicated by the order of the averaged ranks on all five tasks. These findings are in good agreement with Warren et al. (1969) report that frontal cats with severe degeneration in MD are more severely retarded in reversal learning and more highly resistant to extinction than cats with frontal lesions that caused only mild or moderate degenerative changes in MD.

No convincing evidence that the size of the frontal lesions had an important effect on the amount of behavioral loss was obtained on any other learning task. Frontal 57, for example, learned 5 sec delayed response in the WGTA in fewer trials than seven of ten normal cats and in less than half as many trials as frontal 41 with a smaller lesion. A comparable lack of correlation between the amount of damage to proreal and pericruciate cortex and impairment in delayed response learning was reported by Warren, Warren and Akert (1962) and by Wikmark (1970). Both the present experiment and that of Warren et al. (1962) failed to demonstrate a positive relation between lesion size and impairment in double alternation performance.

TABLE VII

Summary of experimental design

Test days	Phase	Stimulus
1–4	Control	None
5	Humans	Chair
7		Human sitting passively
9		Human who pets cats on approach
11		Human holds cat on lap at start
13		Human holds and pets cats
15	Animals	Empty plexiglas cage
17		Rat in cage
19		Pigeon in cage
21		Male cat in cage
23		Female cat in cage
26		Marble and pop beads
28		Noise ball
30		Dinosaur
32		Noisy, moving dinosaur
34	Unfamiliar foods	Catnip
37		Fish roe
39		Pigs feet
41		Tuna fish
43		Beef kidney
45–49	Food deprivation	None
50–51	Control	None

TABLE VIII

Ranks of frontal cats on reversal learning tasks

	Lesion size									
	Larger			Smaller						*p*
	57	59	63	41	48	68	56	62	65	
Spatial reversals										
Experiment 1	6	8	9	5	1	2	7	3	4	0.024
Experiment 2	9	6	8	5	4	1	7	3	2	0.024
Experiment 16	8	1	4	3	2	5	6	7	—	—
Perseverative interference										
Experiment 17	7	6	4	1	2	3	5	8	—	—
Visual reversals										
Experiment 26	5	6	—	3	4	1	2	—	—	0.067
Perseveration index	9	8	7	4	1.5	1.5	5	6	3	0.012

The ranks of the frontal cats on six measures of activity described in this paper are given in Table IX, which indicates that both of the cats with larger lesions were more active than the frontals with smaller lesions only in terms of absolute level of activity in the open field (measure *a* for Experiment 19). In contrast to the results of the learning experiments, there is no strong suggestion that the larger lesions produced a more extreme effect on activity than smaller lesions.

TABLE IX

Ranks of individual frontal cats on activity tests

Experiment and response measure	Larger lesions		Smaller lesions			
	57	59	41	48	68	56
18. Total score	6	1	2	5	3	4
19*a*. Total score for Days 4–30	5	6	4	2	3	1
19*b*. Per cent decrement (Days 1–3 vs. 4–30)	4	5	6	3	2	1
20. Score for Days 1–20	6	3.5	3.5	1	5	2
25. Score for Days 1–5	6	1	4	3	5	2
26. Total score	5	3	4	1	2	6
Overall rank	6	3	5	1	4	2

CONCLUSIONS

Research on the frontal cats summarized in this paper and in Warren (1964) indicates that the effects of subtotal removals of frontal association cortex are similar in several ways to those observed in rhesus monkeys with frontal lobectomies:

1. Frontal cats and monkeys are frequently impaired on discrimination reversal tasks which favor the occurence of perseverative interference.
2. Frontal cats and monkeys manifest transient impairments in double alternation performance.
3. Both frontal rhesus macaques and cats are retarded in post-operative acquisition of active avoidance responses in a two-way shuttle box.
4. Frontal cats, like frontal monkeys, are sometimes deficient in the rate of habituation to novel stimuli.
5. Both frontal cats and monkeys show a decrease in aggression in social behavior post-operatively.

Warren (1964) mistakenly construed an experiment by Brody and Rosvold (1952) as indicating that frontal lesions increase aggression in rhesus monkeys. It is now clear that frontal lesions generally result in a reduction in aggressive behavior in monkeys (Batuyev 1969, Butter et al. 1970, Deets et al. 1970, Snyder 1970) so that, allowing for species differences in social behavior patterns, one must regard the effects of frontal decortications on social and affective behavior as more similar than not in the two species.

Frontal cats with subtotal lesions that largely destroy gyrus proreus differ from frontal monkeys in two major respects:

1. Frontal cats unlike rhesus monkeys are not generally hyperactive.
2. Cats with lesions in gyrus proreus and adjacent frontal areas are not reduced to a chance level of performance in either the WGTA or in variants of the Nencki Testing Situation, as is the case with frontal rhesus monkeys (Ławicka and Konorski 1961, Warren et al. 1962, Divac 1968, 1969, Thompson 1968, Wikmark 1970, Divac and Warren 1971).

One is tempted in comparative research to emphasize the differences rather than the similarities among species. It would be foolhardy, however, to maintain on the basis of the present results that the functions of the frontal association cortex are fundamentally different in cats and rhesus monkeys. Even though some frontal cats may perform as well or better than some normal animals in learning delayed response postoperatively, the performance of frontal cats is significantly inferior to that of normal animals under more demanding conditions (Warren 1964, Wikmark 1970). Conversely rhesus monkeys may attain substantially better than chance scores on delayed response tasks under a variety of conditions (Battig et al. 1960, French and Harlow 1962, Blake et al. 1966, Cianci et al. 1967, 1969, Pinsker and French 1967, Divac and Warren 1971). The difference between species thus appears to be quantitative rather than qualitative.

There is a second major reason why we are reluctant to claim that the functions of the frontal cortex are dissimilar in cats and rhesus monkeys on the basis of available evidence. The frontal syndrome observed in lobectomized rhesus monkeys has been fractionated into a set of specific symptoms that are correlated with the destruction of particular foci within the frontal cortex. Lesions in the posteromedial portion of the orbital frontal cortex, but not elsewhere in the frontal lobe, produce an exaggerated resistance to the extinction of operant responses (Butter 1969). Ablation of the inferior convexity, but not of the medial orbital cortex, produces a profound impairment in differentiation learning (Iversen and Mishkin 1970). Ablations of either the inferior convexity or of orbital cortex occasions a deficit in visual discrimination reversal learning (Butter 1969, Goldman et al. 1970), but the effects of the two lesions differ in respect to the duration of the impairment and the type of errors made (Iversen and Mishkin 1970). Rhesus monkeys with lesions in sulcus principalis are impaired on delayed alternation, but not on a conditional position response, while animals with lesions in the arcuate sulcus are impaired in learning the condi- disrupt the retention of differentiation habits learned with symmetrical (Goldman and Rosvold 1970).

A similar segregation of functions has been demonstrated in dogs. Destruction of the medial frontal cortex selectively impairs differentiation with asymmetrical reinforcement, lesions in the orbital gyrus disrupt the retention of differentiation habits learned with symmetrical reinforcement, and ablation of gyrus proreus impairs delayed response in dogs (Dąbrowska 1971).

We do not know what region within the projection field of MD in cats is analogous to the principal sulcus in rhesus monkeys. Since none of the behavioral experiments with cats, including the present study, has been done with animals that had sufficiently large cortical lesions to produce complete degeneration in MD, we can not ignore the possibility that the partial preservation of delayed response capability in our cats is due to sparing of a critical subregion within its prefrontal cortex.

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