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THE EFFECT ON AFFECTIVE AND COGNITIVE BEHAVIOR IN THE DOG OF LESIONS OF THE PYRIFORM-AMYGDALA-HIPPOCAMPAL COMPLEX[1]

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It has been reported that affective responses are usually more intense in cats (but sometimes less) after than before lesions in the temporal lobe (1, 11, 13), and that they are usually less intense in monkeys (but sometimes more) after than before lesions in analogous structures (4, 5, 10). Although the inconsistency in the results has generally been attributed to differences between species, there is no evidence that a similar inconsistency may not appear within a species as a result of different genetic or developmental history. One purpose of the present paper is to investigate the effect of similar temporal lobe lesions on the affective behavior of dogs having different genetic or developmental histories. Another purpose is to compare these effects in the dog with those which have been obtained in monkeys and cats.

It has also been reported (7) that impaired performance in visual discrimination, but not in delayed-response-type problems, is evident in monkeys following temporal lobe lesions. The performance on discrimination tests, as well as that on other problem-solving tasks, has not been investigated in other species following temporal lobe lesions. The second purpose of this paper is to study the effects of such lesions on the dog's performance in problem-solving tasks.

METHOD

Subjects

The life histories of the seven experimental animals are summarized in Table 1. Controls were litter mates of the same sex and matched as nearly as possible in preoperative behavior. The treatment for each control was the same as for its operated mate except in surgery, where brain tissue was not removed though all other procedures were identical.

The cocker spaniels, the beagles, and the female terriers had been tested before operation on a battery of tests which had been standardized on a large population of intact dogs in an experiment on the genetics of behavior. They were retested on the same battery of tests after operation. The male terriers were operated in infancy and tested at maturity. Most of the behavioral observations were made at Bar Harbor. The animals were shipped to New Haven for a six-week period of observation, surgery, and recovery.

Procedure

Surgery. Animals were anesthetized with a 10 per cent sodium amytal solution (0.6 cc/kg body weight) administered intraperitoneally. With aseptic technique a skin incision was made in the temporal region extending from below the zygoma backward to a point approximately halfway between the external auditory meatus and the vertex. The zygoma was removed and the temporal muscle split. The skull was opened by enlarging a burr hole to create a defect about 1½ in. in diameter. The dura was opened in a cruciate fashion, exposing pseudosylvian and posterior ectosylvian regions. By means of an 18-gauge sucker the periamygdaloid cortex was resected subpially. The excision was extended into the depths to remove the entire amygdaloid complex, care being taken to spare the optic tracts which lie immediately beneath. This excision afforded entrance to the lateral ventricle. A curved retractor was used to spread apart the walls of the ventricle, affording a clear view of about one-half of Ammon's formation (hippocampus). The visible portion was sucked out and the excision extended as far as it was deemed safe mediodorsally along the floor of the ventricle. Closure was made in a routine fashion by the interrupted silk technique. After allowing about two weeks for recovery, the surgical procedure was repeated on the second side. Recoveries were uneventful except for inflammation of the left eye of 985, which blinded that eye.

Anatomical procedures. After postoperative training had been completed, all animals were killed with intravenous Nembutal and, after perfusion through the aorta with normal saline followed by 10 per cent formalin, the brains were removed and prepared for sectioning, stained, and reconstructed as described by Pribram and Bagshaw (8).

Testing. The following eight special tests and observations were made: food intake, social dominance, sexual behavior, maternal behavior, handling test, reactivity test, discrimination and delayed response test, and spatial orientation test. All the tests were not completed on the first two pairs of animals. The procedure for these tests has been outlined in detail in a mimeographed manual (12); a brief description of each procedure is given here in connection with the results.

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TABLE 1
Subjects

Dog No. (Operate)	Dog No. (Control)	Breed	Sex	Age at Operation (months)	Age at Sacrifice (months)
985	986	Cocker spaniel	M	13	22
1192	1191	Cocker spaniel	F	15	32
1336	1337	Cocker spaniel	M	17	25
1649	1650	Wire-haired terrier	M	2	18
1857	1858	Beagle	M	14	21
1859		Beagle	M	14	21
1903	1904	Wire-haired terrier	F	13	20

RESULTS

Food Intake

Procedure. Ordinarily the dogs were kept in individual cages supplied with Purina Laboratory Chow and water. The animals were allowed to exercise in an outdoor field for approximately 7 hr. per day. The beagles and female terriers were tested preoperatively and late postoperatively, by another procedure, in which the dogs were tied up twice daily in an outside group-living pen and allowed to feed from individual dishes.

Results. The average daily food intake of five dogs before surgery was 286 gm.; for the two immediate postoperative weeks, 571 gm.; and for the second postoperative month, 276 gm. No such enhancement was observed in the controls, whose corresponding values were 283, 286, and 274 gm. Since there was some irregularity in gathering data from different animals because of transportation problems, a day-by-day comparison of each *S* with its control affords a more valid comparison than overall averages. During the preoperative period the pairs appeared to be fairly well balanced, and experimentals exceeded controls in 35.5 out of 58 paired comparisons. During the immediate postoperative period, 59 out of 63 comparisons favored the experimentals, but in the late postoperative period the experimentals were higher in only 28 of 78 matchings. The imbalance was produced chiefly by one animal, and thus depressed food intake should not be considered as a characteristic feature of the chronic amygdalectomized dog. All the *S*s showed great day-to-day variability in food intake, but the striking increase during the first two weeks following surgery is shown by the fact that in 59 out of 63 comparisons, the intake of the operate is higher than that of its control. The increased intake was reflected in a temporary increase in weight of the experimental animals.

Social Dominance

Procedure. Dominance in this experiment was defined as the ability to hold possession of a bone in a competitive situation. In all cases the dominant member of a pair in the preoperate dominance tests was operated; the subordinate was maintained as a control. Two tests were used, paired and group. In the paired test two animals were observed for 10 min. At the end of this time the bone was given to the subordinate animal to see whether it would retain possession when given this initial advantage. In the group test a bone was tossed to the entire assemblage after the attention of all members had been secured. One animal usually took complete possession within 2 min. At 2 min. this animal was removed and the test was repeated with the remaining *S*s, and so forth, until only one was left. The animals were returned to the group one by one in reverse order.

Results. After surgical treatment of the dominant member of each of six pairs, social rank as measured in the paired test was reversed. The male terrier, operated as a juvenile, was subordinate to its intact brother when tested as an adult.

The lower social status of the operated animals was also evident in the group tests the results of which are summarized in Table 2. Only two exceptions, noted by asterisks in the table, were found. Both related to operated 1192, which was dominant over a much younger and smaller male terrier one day after the terrier had arrived in Bar Harbor. The second reversal occurred while 1192 was in estrus.

The dominance relationship between dogs is more complex than can be indicated from the results of the bone test alone. As an example, it may be noted operate 1649 mounted control 1650 during homosexual episodes, although control 1650 was definitely dominant as judged by the bone test. Another peculiarity of the dominance relationship of this pair is illus-

TABLE 2

Summary of Dominance Relationships in Two Social Groups

Numbers indicate position on bone test.

Group 1 (all tests postoperate)

Subject No.	Subject Group	Sex	Dates 1950–51 7-15	7-17	9-7	9-11	9-13	6-27	Mean
987	Control	M*			3	2	2	4	2.7
1191	Control	F	1	1	1	1	1	2	1.4
1192	Operate	F	2†	3	4	4	4	3‡	3.3
1649	Operate	M	4	4	5	5	5	5	4.7
1650	Control	F	3	2	2	3	3	1	2.3

Group 2

Subject No.	Subject Group	Sex	Before Operation Dates 1952 6-18	6-19	6 20	6-21	Mean	After Operation Dates 1952–53 8-22	8-26	9-24	1 18	Mean
1857	Operate	M	4.5	4.5	5	4	4.5	5	3	5	3	4
1858	Control	M	4.5	4.5	3	3	3.2	1	1	2	1	1.2
1859	Operate	M	1	2	3	1	1.5	4	5	3.5	4	4.1
1903	Operate	F	2	1	1	2	1.5	3	4	3.5	5	4.1
1904	Control	F	3	3	4	5	3.2	2	2	1	2	1.8

* Castrate male.

† Number 1192 on home territory, 1650 newly introduced to group.

‡ Number 1192 in heat.

trated by a note made at the time of the bone test when the dogs were a year old.

"Experimenter has many times seen operate 1649 fight as fiercely as control 1650, and even drive control 1650 under the house if operate 1649 were attacked. Apparently, however, he will not take the initiative, i.e., is not the aggressor, but if challenged—actually attacked—can fight as well or better than control 1650, and appears dominant over him when and if an actual fight occurs." Similar observations were made over and over again.

Sexual Behavior

Procedure. The sexual behavior of males was observed during periods of 10 min. with a receptive female. Three to four periods of observation were conducted before and after surgery. The acts which are characteristic of the mating behavior of this species were checked as they occurred during each minute of the test. A numerical system of rating both males and females has been established, but for the purposes of this paper a descriptive account of the results is sufficient.

Results. Each of the five adult males was tested pre- and postoperatively. Three individuals (1836, 1857, 1859) were unchanged in their sexual behavior, the similarity extending even to details of the courtship pattern. The fourth adult male (985) was especially excitable sexually before surgery, but on six postoperative tests he appeared to be completely unresponsive. The one male operated on as a juvenile was notable for the development of homosexual behavior with his control. The operated *S* assumed the male role; erection was frequently observed, but not ejaculation. Gradually the frequency of such relations decreased, and there are no records of their occurrence after 10 months of age. This homosexual relationship appeared to be specific for there were no advances toward a castrate male living with the pair, toward other males, or to bitches not in heat. Although occasional homosexual relationships have been observed among some hundred litters living under similar conditions, this relationship was unique in its intensity and frequency. Both this operate and his control responded to bitches in heat in the usual male

pattern. However, the operated animal was slower to develop an erection, and was more readily driven off by a female that showed aggression.

The operated female 1192 came into heat during the postoperative observation period. She was normally receptive, became pregnant, and reared a litter of puppies successfully.

Handling Test

Procedure. Each *S* was placed alone in its ordinary living quarters where a person familiar to *S* approached, called, and handled *S* in a standardized fashion. The responses of the animal were recorded both by the handler and an observer. For purposes of summarizing and comparing responses a scoring and classification system has been developed for five categories of responses: timidity, aggression, investigation and attention-seeking, tail-wagging, and attraction to the handler. Tests were conducted at one year of age and about six weeks following the second operation.

Results. The results of this test are summarized in Table 3. The average responsiveness of the experimental animals was reduced in each category, except for investigative behavior. The significance of the preoperate differences between control and experimental groups and the significance of the changes in responsiveness following treatment were evaluated by the Mann-Whitney *U* test (6). None of the pretreatment differences between operated *S*s and controls are significant; the decrease in tail-wagging ($p = .01$) and attraction ($p = .02$) was significantly greater in the operated group. The decrease of aggressive responses is also notable, but, in contrast to the general trend, the greatest increase in aggressive responses was found in one animal of the operated group, thus confusing the statistical test. If the *amounts of change* both in aggressiveness and in timidity are ranked in order of size regardless of sign, these differences are significant at the .01 level, with the amount of change greater in the experimental group.

Reactivity Test

Procedure. This test is modified from the procedure described by Fuller (2). The dog is restrained by loose-fitting loops around its legs, and is prepared for recording the pneumogram, electrocardiogram, and electromyogram from the thigh. The animal is observed during

TABLE 3

Effects of Brain Lesions on Performance in the Handling Test*

	Timidity		Aggression		Investigation		Tail-Wagging		Attraction	
Operated	Before	After	Before	After	Before	After	Before	After	Before	After
985	47	34	5	0	7	2	36	6	11	8
1192	40	30	7	0	0	10	36	27	13	10
1336	21	20	12	10	16	12	27	27	16	10
1649		33		2		1		0		5
1857	69	52	6	24	0	0	53	25	16	4
1859	43	68	23	1	0	0	41	12	11	7
1903	61	48	25	1	0	0	32	6	13	1
Mean	47	42	13	3	4	4	38	17	13	7
Control										
986	54	54	2	2	0	0	15	15	11	11
1191	28	28	5	17	13	7	33	24	13	16
1337	24	31	11	11	17	12	27	27	13	13
1650	7	14	13	15	13	11	24	21	13	8
1858	44	31	22	13	9	0	39	30	12	12
1904	55	35	19	16	6	0	38	55	13	8
Mean	35	32	12	12	10	5	29	32	13	11

* The "before" tests were performed at one year of age. The "after" tests were done about three weeks after the second operation.

periods of isolation, which are interposed with the following episodes: *E* enters and speaks gently to dog; loud bell rings for 30 sec.; four single induction shocks are applied to the left hind leg; *E* enters and threatens the dog while forcing *S* into prescribed positions. The overt behavior of the *S*s is checked on a record form. This includes (*a*) position of body and tail carriage, (*b*) tension responses (lip-licking, muscle tension, vocalization, and panting), (*c*) investigatory behavior toward surroundings or toward *E* when he is working with *S*, (*d*) tail-wagging, (*e*) response to restraint including straining against the loops and active struggling, and (*f*) biting. Weights are assigned to these behavior patterns in proportion to the energy level of the responses, and the sum of these weighted scores is called the E score. A low E score will characterize a passive animal, a high E score one which is active.

Results. Both experimental and control groups showed considerable individual variability on this test. No physiological or overt behavior characters were found to differentiate the two groups, nor did the surgical treatment produce any consistent changes in total score or in specific forms of response.

Discrimination and Delayed Response

Procedure. The apparatus for these tests was a T-shaped enclosure designed so that *S* could select the proper exit corridor by responding to the movement of distinctively marked panels, located at the angles of the T. The test involves movement rather than form discrimination, and the cue is distinctive enough to be readily perceived by normal dogs. Food was given when the animals emerged from the apparatus. Learning in the situation was evaluated by the runs criterion of Grant (3) or by the chi-square test applied to cumulative trials, using the .01 significance level as the criterion. The delayed response test utilized the same procedure except that a delay was interposed between stimulus and the opportunity to respond. During this interval the starting-box door was covered by a curtain. The .05 significance level was used as criterion for the delayed response test.

Results. Six operated dogs (all with surgery at maturity) had met the discrimination test criterion. After surgery only operated 1336 achieved the criterion during retraining. The other operated animals moved very slowly in the test situation and frequently failed to eat at the end of a trial. Operated 1192, 1336, 1859, and 1903 had met the delayed response criterion before operation, but only 1336 was successful on retest after operation. However, this delayed response test is dependent upon movement discrimination; therefore, poor performance on this test cannot properly be attributed to a delayed response deficit.

Spatial Orientation Test

Procedure. The apparatus for this test was set up in the exercise area of a group of dogs so that they might become thoroughly familiar with it. It consisted of a goal table about 3 ft. high, which could be approached from three sides—one (D) a direct steep ramp; another, a straight (S) elevated path consisting of a ramp, low table, and connecting bridge; and the third, a similar elevated path with a single turn (L) in it. An opaque screen, open on only one side, fitted on the goal table and was turned so that only one of the three paths was open on a given trial. A reward of canned fish was placed in a dish on the goal table. Preliminary training was carried on to a criterion of three consecutive successful trials in each of the pathways, only one path being available on each trial. In the actual testing all three ramps were in position, and the dog was required to find the correct one. Thirty-six trials were given over six days. On the fourth day the apparatus was rotated 180° from the position used on the first three days. Errors and time scores were recorded for each trial. On the seventh day an extinction test was given in which the goal was blocked off. The number of attempts to reach the goal table within 5 min. was recorded. Four *S*s had only postoperative training on this test, three were tested both pre- and postoperatively.

Results. Four *S*s received only postoperative training. Number 985 did not meet the preliminary training criterion within the 36 trials; the others met this criterion but did poorly in the actual test. The number of failures out of 36 trials were: 1192, 34; 1336, 13; 1649, 22. In 100 dogs trained on this apparatus in other studies the range of failures has been from zero to 3 out of 36 trials.

TABLE 4

Effects of Amygdalectomy on Spatial Orientation

The first figure of each pair is the preoperative value; the second figure is postoperative.

Dog	Failures	Average Errors Per Set of Trials	Average Time per Trial Sec.	Extinction Resistance
Operates				
1857	0–6	14–11	8.4–14.8	25–5
1859	0–0	14–7	7.8–10.5	39–6
1903	0–27	18–*	13.2–20.4	31–0
Controls				
1858	0–1	18–7	9.9–6.7	17–12
1904	0–8	16–6	13.4–10.2	31–21

* Could not be estimated because of failures to attempt a solution.

The results on three operates and two controls which were given tests before and after operation are summarized in Table 4. In both groups there is evidence of some lowering of motivation, as shown both by an increase in the number of failures and a decrease in the number of approaches to the goal during the extinction trial. Both these effects are greater in the experimental *Ss*. The experimentals also show increased time on the postoperative tests, while the intact animals had decreased time on their second series of tests. When the experimental animals performed, however, there was no evidence of increased error scores.

Anatomical Results

The size of the lesion varied considerably, being smallest in 985 and largest (about equally) in 1192, 1649, and 1857. In every case Ammon's formation is destroyed except in its most posterior portion. The amygdala and periamygdaloid cortex is destroyed except in 985, where there is some sparing of the periamygdaloid cortex in the medial anterior portion of the lesion, and in 1859, where there is some sparing of the lateral portion of the periamygdaloid cortex anteriorly.

Incidental Observations

Changes in attitude during handling and in attraction to people during regular inspection were noted in several *Ss*. Number 985 was an extremely submissive animal before surgery. Afterward he no longer cowered at the approach of a person, but "presented a stolid, phlegmatic appearance." A similar postoperative unresponsiveness was noted in 1191, 1857, 1858, and 1903, each of whom deviated from a characteristic preoperative positive response to humans. Individuals previously familiar with the *Ss*, but who did not know the group assignments, were readily able to distinguish operated and controls by observing them a few minutes in their living quarters. The one exception was 1336, whose behavior was not noticeably affected. The operated animals tended to keep away from the handler and remain behind the control *Ss*. However, submissive forms of behavior such as crouching, rolling over on back, and shivering were greatly reduced, although these patterns are characteristic of dogs which avoid people.

In two instances the release of a rage pattern was sporadically observed. Numbers 1859 and 1903 would, when startled, turn savagely on their handler, though such episodes were always of short duration. Number 1903 also became extremely aggressive towards her intact living companions postoperatively, a characteristic which is not unusual in wirehaired terriers. In the formal dominance tests 1903 was submissive to the animals she attacked. The occurrence merely shows that the brain lesion did not eliminate aggressive behavior.

DISCUSSION

It is indicated in the results of this investigation that, in general, the effect of temporal lobe lesions on the dog is similar to that on the monkey. As with the monkeys described by Rosvold, Mirsky, and Pribram (10), the dog which is dominant before operation is not dominant after operation. However, as illustrated by operated 1192, transient social and physiological factors (as in the monkey) may alter the general relationship. It is also apparent in the behavior of these operated dogs that the effect is not simply one of decreasing "aggressiveness" for there are circumstances in which these dogs are as aggressive as any at the laboratory. It seems, rather, that the effect of the operation is to make the dog less responsive to stimuli in general though not incapable

of responding appropriately to stimuli when they are persistent enough to elicit a response. There is no evidence in the results of this study to support the contention that after temporal lobe operations in dogs, as is usually the case in cats, affective responses are more intense. The only suggestion of such a condition is in the two dogs which, when startled, turned savagely on their handler, though such episodes were always of short duration. At other times, affective responses in these dogs, as in the other operated *S*s, were reduced after surgery.

This study, like that of the social behavior of monkeys, indicates that contradictory results may be obtained from a study of the effects of brain lesions on behavior depending on the circumstances in which the behavior is observed. The dogs of this study are less timid after operation when observed reacting toward their handler. When reacting toward other dogs in a competitive feeding situation, however, they are no longer dominant but noncompetitive, a condition which might have been interpreted as more timid. Similarly, the reactivity test which measures physiological responses to emotion-provoking situations does not differentiate operates from nonoperates; whereas, the handling test which measures the animals' reactivity to the handler in emotion-provoking situations clearly differentiates the two groups.

The consistently abnormal sexual behavior of monkeys following temporal lobe operations reported by Klüver and Bucy (4, 5) and Schreiner and Kling (11) is not apparent in these dogs. One dog of this study was completely unresponsive to sexual stimuli after operation, a condition similar to that in monkeys after large temporal lobe lesions observed by Rosvold and Freedman (9). The dog operated as a juvenile responded sexually to his male control more intensely and frequently than observed in any other animal in this laboratory. He did, however, respond normally to bitches in heat. The sexual behavior of the other dogs in the series was apparently unaffected.

The dogs of this study, like the monkeys described by Mishkin and Pribram (7), showed, with one exception, a gross impairment in performance on the discrimination-type test after operation. This is consistent with the opinion that there is a focus for visually guided behavior in the inferior ventral temporal lobe. The lesions of the brains of the dogs in this series, though mainly medial, extended into lateral cortex presumably homologous to the inferior temporal region of the monkey. It is even possible that the whole syndrome results from such an impairment, since the tests showing no differentiation between operated and controls were those in which vision is of subordinate importance.

There do not appear to be any differences in the lesions which would account for the differences in behavior.

Since the number of cases representing each breed is small, the relationship between breed differences and the differences in effect of the lesion on behavior cannot be determined from the results of this study. However, the changes appeared to be more severe in the case of the terriers than in cocker spaniels and beagles. It is emphasized, however, that the postoperative behavior of some operated animals was no more extreme than that of some intact animals at the laboratory. Since conditions of rearing and experience are relatively constant for all the dogs, it is suggested that inherited or very early acquired neural organization may be as effective as brain damage in determining the effective behavior of a particular member of a species.

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