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INFLUENCE OF AMYGDALECTOMY ON SOCIAL BEHAVIOR IN MONKEYS[1]

H. ENGER ROSVOLD, ALLAN F. MIRSKY, AND KARL H. PRIBRAM

Department of Psychiatry and Laboratory of Physiology, Yale University, and Department of Neurophysiology, Institute of Living

Several authors (2, 4, 5) have reported that temporal lobe lesions result in changes in social behavior of monkeys. Since these investigators were only incidentally interested in social behavior, they reported only summary descriptions of their methods or results. It is generally impossible to determine from their reports on what basis they arrived at their conclusions and what, in fact, they meant by social behavior. Therefore, a series of studies using a uniform method of observation has been undertaken to relate brain function to social behavior in monkeys.

Brody and Rosvold (1) reported in detail a method for studying the effects of frontal lobotomy on the social interaction in a colony of *Macaca mulatta*. A similar method was used in the present study of the effects of a temporal lobe lesion on social interaction among monkeys. In addition, the behavior of each monkey, when housed separately, was observed.

METHOD

Animals

Eight young male rhesus monkeys, ranging in weight from 2.90 to 3.85 kg, were housed for a total of 18 two-week periods alternately, either separately in individual cages or together in a large group cage, according to the temporal sequence designated in Table 1. The individual cages were 2 ft. by 2½ ft. by 2½ ft. The group cage was 7½ ft. by 4½ ft. by 6½ ft. and included a movable partition at the center, thus permitting the large cage to be divided into two smaller cages 3¾ ft. by 4½ ft. by 6½ ft. When the monkeys were housed individually, they were fed Rockland monkey pellets and peanuts, one at a time, through the wire mesh of the cage front. When the monkeys were in the group cage, either pellets or peanuts were introduced, one at a time, through a feeding device consisting of a length of 1½-in. pipe mounted obliquely on a stand so as to extend 1 ft. into the large cage. It was fitted at the animals' side with a can containing a small opening large enough to admit only one monkey's paw. At the end of the observation hour, additional pellets were thrown into the group or individual cage, as the situation required, in amounts sufficient to make up the total daily ration of 80 cal/kg body weight per animal. This diet was supplemented three times a week with one-half orange per animal.

Observational: Group Cage

When the animals were together in a group cage, one *E* observed them at the same time each day for 1 hr. during the peanut-feeding situation. Four hours later another *E* observed while introducing the pellets. Food was also frequently offered directly to one or another of the animals, or placed between two monkeys of the group. Diary records were kept of group behavior, and when the typical group interaction had been reliably described, the most dominant—i.e., the highest animal in the hierarchy—was subjected to a two-stage bilateral amygdalectomy. Two other animals were operated on at two-month intervals. During the two weeks allowed for surgery and recovery, all animals were housed individually.

During the latter half of six of the two-week group-cage periods, alterations in group size and living space were instituted to increase interaction and to isolate those parts of the group in which the hierarchy was not clear for more intensive study. In addition, food was withheld from the colony at various times for 48 or 72 hr.

Observational: Individual Cages

At the same time on each day of the individual-cage periods, one *E* observed each monkey while offering it three peanuts. Four hours later, another *E* observed each animal while offering it five pellets. During period 1, diary records were kept of each animal's behavior. At the end of this period, and before placing the animals together for the first time in the group cage, the two *E*s independently ranked the eight animals in order of aggressiveness and/or fearlessness.[2] On each day of succeeding individual-cage periods the monkey's behavior was rated according to the categories listed in Table 2. The total score was used as a measure of the aggressiveness of each animal.

Surgical and Anatomical Procedures

A two-stage myoplastic craniotomy was performed on three of the animals; they were anesthetized with 0.8 cc/kg of a 5 per cent solution of Nembutal injected

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[2] Hereafter ratings of individual-cage behavior will be labeled "aggressiveness." They probably could equally as well be labeled "fearlessness." The definition is according to the categories listed in Table 1. In the group-cage situation, however, "aggressiveness" has the objective behavioral referrant of one animal attacking or threatening another.

TABLE 1

Temporal Sequence of Observation Periods

DESCRIPTION	NUMBER (2-wk. periods)	CAGE SITUATION
Preoperative period	1	I
	2*	G
	3	I
	4	G
	5	I
	6	G
1st operation	7	I
1st postoperative period	8*	G
	9	I
	10†	G
2nd operation	11	I
2nd postoperative period	12	G
	13	I
	14*, §	G
3rd operation	15	I
3rd postoperative period	16	G
	17	I
	18*, †	G

Note: *I* refers to individual cage; *G* refers to group cages.

* Large cage divided in two, top four animals in one, bottom four in the other.

† Cage space reduced by one half.

§ Most submissive animal in the group removed from the colony.

TABLE 2

Individual-Cage Behavior Scoring Scheme

CATEGORIES	RATING AND DESCRIPTION
Vocalization	Noisy-loud = +2
	Soft noises = +1
	Silent = 0
Position at start of of feeding	At front of cage = +3
	Goes from front to middle (back) = +2
	At middle of cage = +1
	At back of cage = 0
Pellet taking	One + for each taken, up to 5. If none taken = 0
Behavior after taking pellets	Stays at front for all pellets = +2
	Retreats after each to middle of cage = +1
	Retreats after some but not all = +1
	Retreats after each to back = 0
Threatening behavior	Jumps at *E* during feeding = +2
	Teeth baring or grimacing = +1
	Neither = 0
Flight behavior	Animal makes as if to escape = −1 for each time it occurs

Note: Aggressive toward *E* = high positive score (max. +14); fearful of *E* = low positive or negative score.

intraperitoneally. In each case, the left side was operated first and the right side a week later. A semilunar incision was made over the zygoma, curving forward over the orbit. Temporal muscle was split and the zygoma excised. After a burr hole had been enlarged to expose the orbit and temporal fossa, the dura was opened in a cruciate manner. The temporal lobe was retracted, thus exposing the periamygdaloid region just medial and posterior to the Sylvian fissure. An 18-gauge sucker was inserted into the amygdala, and the entire formation removed subpially downward and backward as far as the temporal horn of the ventricle and medially as far as the brain stem. Bleeding was controlled by packing and cautery, and the wound was thoroughly irrigated before closing the dura. Fascia was closed in layers with interrupted silk technique and the scalp with continuous subcuticular stitch.

When the behavioral observations had been completed, the operated animals were sacrificed and their brains prepared for histological examination as described by Pribram and Bagshaw (4).

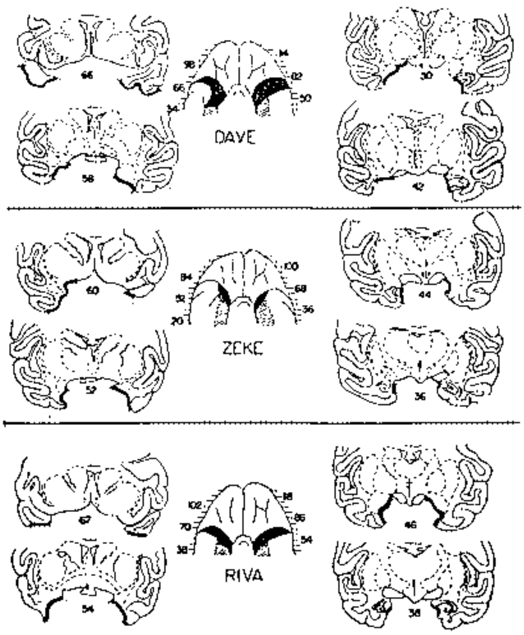

FIG. 1. Representative cross sections and reconstructions of brains of operated animals. Black indicates lesion, xxx indicates spared amygdala, oblique lines indicate spared Ammon's formation.

RESULTS

Anatomical

The reconstruction of the lesions is illustrated in Figure 1. The lesions in the three animals were approximately bilaterally symmetrical. In Dave's brain, in the right hemisphere, the medial portion of the temporal polar cortex, together with all of the amygdaloid complex except for a small portion of the lateral nucleus, was resected. Posteriorly, this lesion invaded the uncal extremity of Ammon's formation. In the left hemisphere, the lesion in the temporal polar cortex was

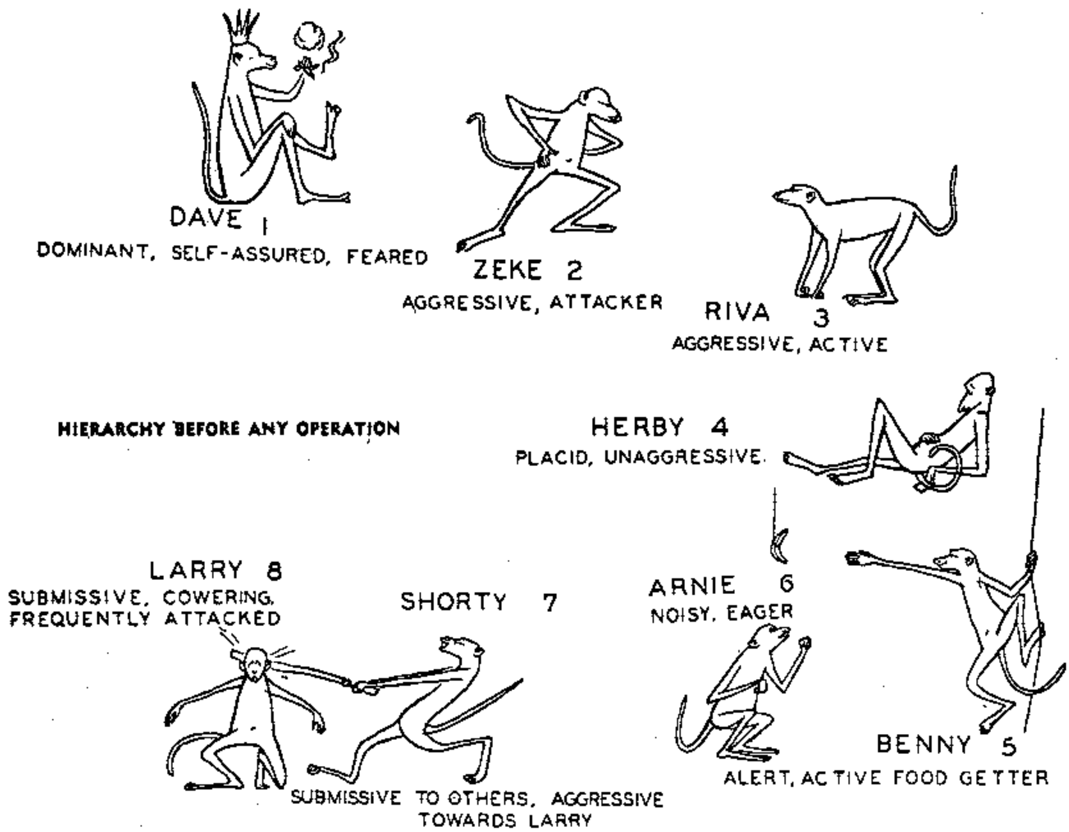

FIG. 2. Hierarchy before any operation

slightly more extensive laterally, a little more of the basolateral amygdala was spared, and Ammon's formation barely touched on its ventromedial surface.

In Zeke the temporal polar cortex was barely invaded on either side. The corticomedial group of amygdaloid nuclei was completely resected bilaterally, but a small portion of the basolateral group remained intact. The posterior end of the lesion barely touched Ammon's formation.

In Riva the lesion invaded the temporal polar cortex bilaterally, and again the corticomedial nuclei of the amygdala were completely resected. However, the basolateral group of nuclei was fairly extensively spared on both sides. The uncal extremity of Ammon's formation was slightly injured on its ventromedial surface.

Group-Cage Behavior

By the second group-cage period a dominance hierarchy was firmly established on the basis of primacy in food getting and such other dominant behavior as aggressive chasing, biting, and threatening gestures. This hierarchy is portrayed in Figure 2.

Within five days after Dave had been operated on, he became submissive to all but Larry. Zeke now monopolized the feeding pipe, dominated the feeding situation, and occupied the preferred floor area of the cage once held by Dave. Toward the end of this period, when the group was divided into top and bottom four, Dave became completely submissive, even to Larry; he avoided other animals, made no attempt to get food, and even refused to accept food from *E*. Attempts to reach Dave's threshold for aggressive response by increasing group interaction were unsuccessful. Even though he would be bitten until blood flowed, he exhibited no aggressive or retaliatory reaction toward the animal that had attacked him.

On the twelfth day after his second operation (the fifth day of group interaction), Zeke

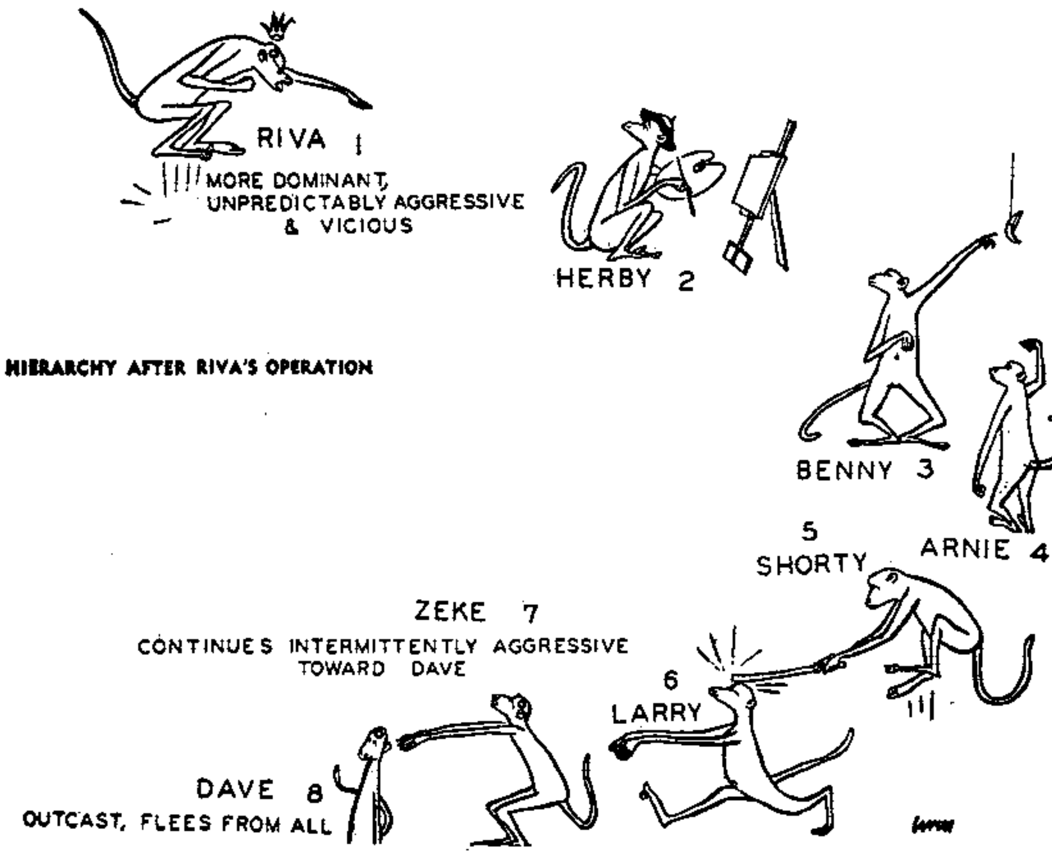

FIG. 3. Hierarchy after Riva's operation

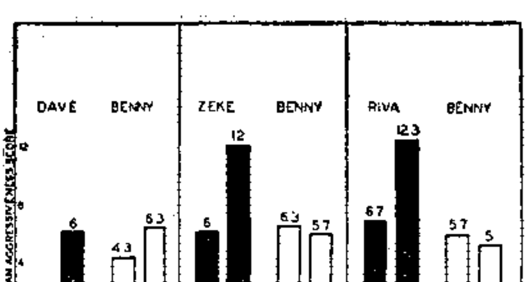

FIG. 4. Aggressiveness in individual-cage situation before and after amygdalectomy. Benny's scores are included for comparison.

became submissive to all but Larry and Dave. Riva now dominated the feeding situation and the food pipe, sharing with no one. Zeke continued to be dominant over Larry and Dave until shortly after the colony was separated into the top and bottom four, when Larry began attacking Zeke. Coincident with this reversal in the Larry-Zeke relationship, Zeke exhibited a tremendous increase in his aggression toward Dave, attacking him almost continuously during the feeding situation. By way of increasing interaction with Zeke, in an attempt to reach his threshold for aggressive response against the other animals in the group, Dave was removed from the colony. This had the effect, *not* of eliciting aggression on Zeke's part, but of eliminating it completely. He now behaved much as did Dave, cringing and fleeing from all, and adopted the tactic of sitting in the corner of the cage and facing the wall.

In contrast to the other two operated animals, Riva did not fall in dominance at any time during the two-month postoperative period. Manipulations of cage space and food deprivation up to 72 hr. were effective only in increasing Riva's aggressiveness. The hierarchy at the end of the experiment is depicted in Figure 3.

Individual-Cage Behavior

The two *E*s agreed significantly better than chance (rho = .95, $p < .01$) on the ranking of the monkeys according to their aggressive behavior in individual cages during the first individual-cage period. This order correlated negatively (rho = −.595; $p = .16$) with the hierarchical arrangement that developed in the group cage. In subsequent individual-cage periods, the rating scheme described in Table 1 was used. Figure 4 shows the mean of the last three preoperative and postoperative scores of each animal. The mean scores of a typical nonoperated control, obtained at the same time, are included for comparison. Two months separate the pre- and postoperative measures in each case. A Mann-Whitney (3) *U* test of the significance of the differences in these comparisons indicates that there were no differences in aggressiveness among the monkeys before surgery. Afterward, the scores of the operates show an increase significant beyond the .01 level of confidence, while that of the unoperated animal shows no change.

DISCUSSION

The results of the present study indicate that following amygdalectomy there are marked changes in social behavior of monkeys. However, there are differences among the animals in the direction and degree of this change.

After surgery all operates, though appearing more aggressive in the individual-cage situation, appeared to be less dominant (in two of three cases) in the group-cage situation. In addition to this difference in direction of effect, there is uniformity of change in the individual-cage situation but not in the group-cage situation.

As evident in Figure 2, the differences in direction and degree of change cannot confidently be attributed to differences among the lesions. If variations in extent of damage to the temporal lobe determined the degree of change in behavior, then Dave should have changed most and Zeke least; this was not so either in the group- or individual-cage situation. It is probable, therefore, that one or more of the discrete structures in the temporal lobe are critical in bringing about the alterations in aggressiveness. Since the degree of change in the group-cage situation, i.e., most in Dave and least in Riva, was consistent only with the extent of damage to the basolateral nuclei, these nuclei may be critical for changes in aggressiveness in the group-cage situation.

The differences in direction and degree of change were consistent with the social environment confronting each operated animal after surgery. Upon return to the colony, Dave was confronted with aggressive and active Zeke and Riva; he fell in dominance. Zeke was confronted with Riva; he too fell in dominance. Riva was faced with relatively submissive nonaggressive animals such as Herby; Riva remained dominant.

The differences in direction and degree of change are also consistent with the length of time preoperatively that the dominance-submission relationships had existed. Dave, who changed immediately after his operation, had elicited submissiveness for only six weeks; Zeke, who maintained the No. 1 position for four days after being returned to the colony postoperatively, had elicited submissive responses for 10 weeks; while Riva, who did not change in status, had elicited submissive responses for 16 weeks.

This study, then, suggests that the pattern of social interaction within the group to which it is returned after surgery and the length of preoperative time the relationships had existed may be as important considerations as the locus and extent of a lesion in determining the effects of a brain operation on the social behavior of a monkey. It is meaningless, therefore, to speak of the effect of an operation on "emotional behavior," "social behavior," and the like, without specifying in detail the conditions in which the particular behavior is observed. And, unless the effect of an operation on behavior is studied in a variety of situations, the findings are at best of limited generalizability.

SUMMARY

1. Eight young male rhesus monkeys were studied in individual and group cages for a period of nine months; during this time, the three animals that were most dominant in the group situation were subjected to bilateral amygdalectomy.

2. There was found to be a negative relationship between aggressiveness in the individual-cage and dominance in the group-cage situation before surgery.

3. After amygdalectomy all animals appeared more aggressive in the individual-cage situation. In the group-cage situation, the same animals, in two of three instances, fell from top to bottom positions in the hierarchy. The third animal suffered no loss in dominance and appeared more aggressive in the group situation after operation.

4. The differences in changes in behavior appear to be related to the social environment confronting each animal upon return to the group after surgery and to the length of time the preoperative relationships had existed.

5. The differences in changes in behavior are not related to the differences in extent of esions as a whole, though they are consistent with differences in damage to the basolateral nuclei of the amygdala.

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