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# BEHAVIORAL CHANGES ASSOCIATED WITH ABLATION OF THE AMYGDALOID COMPLEX IN MONKEYS[1]

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In a frequently cited study, Klüver and Bucy (7) noted striking behavioral changes following bilateral removal of the temporal lobes of the rhesus monkey. These changes were "visual agnosia," changes in dietary habits, increased tendency to examine objects ("hypermetamorphosis"), hypersexuality, and increased tameness. More recently, it has been demonstrated that the temporal lobe of the monkey can be functionally fractionated with respect to some of these general changes. Lesions in the ventrolateral portion of the lobe produce marked impairment in visual discriminations, with no other apparent change (5, 8, 9). Orbito-insula-temporal lesions or more limited anteromedial temporal lesions produce tameness, hypermetamorphosis, and changes in dietary habits without visual discrimination impairment (12, 17). The damaged areas in these latter investigations may be classified among the older or "rhinencephalic" cellular masses. The finding of increased tameness or docility, thus, would be in agreement with the speculation that the rhinencephalon, at least in higher mammals, mediates emotional behavior (11).

As yet, however, very little systematic analysis has been made of behavioral changes in the monkey subsumed under "tameness" or "loss of fear." Generally, conclusions have been based on gross observations of the animals' behavior in the living cages. Furthermore, using other species, some investigators have reported behavioral changes in the direction opposite of tameness following medial temporal lesions (2, 15), although more recent results agree with the changes seen in monkeys (10, 14). Understanding of the behavioral changes may not come until after experimental work isolates the critical relationships; contradictory results may be due, in part, to a lack of control of certain independent variables (such as daily feeding and handling procedures) which are uncovered only after such systematic work. Furthermore, many investigators have failed to report adequate histological reconstructions of lesions, a failing which is important in view of the relatively difficult surgical approach to the medial temporal lobe, the relative crowding of many neighboring units within a small volume (e.g., uncus, body of Ammon's formation, anterior insula, lateral hypothalamus, putamen, etc.), and the ambiguity of some terms used in verbal descriptions of lesions (e.g., anterior pyriform, hippocampal, temporal pole, etc.).

It is the purpose of this paper to attempt a preliminary behavioral analysis of the effects of anteromedial temporal lesions, as well as to substantiate and extend the functional fractionization of the temporal lobe. Two related kinds of questions must be raised in evaluating an assertion that a lesion (or any other independent variable) results in decreased "fear" or "emotionality." (*a*) Are changes found in more than one "emotional" situation? (*b*) Are the "emotional" changes artifactually produced, or at least influenced by other behavioral changes such as altered activity level, paralysis, stupor, blindness, etc.? Two general situations, conditioned avoidance and conditioned depression, produced data which, together with other observations, are relevant to both questions.

## METHOD

### *Surgery*

Each of the *S*s had one of three lesions: experimental animals received a bilateral amygdalectomy and resection of the medical temporal pole (referred to as AM); control animals received either a bilateral resection of the inferior temporal convexity (IT), or a bilateral sham operation (S). All animals were given a rest period of one week following surgery.

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All surgical operations were performed aseptically in one stage, using Nembutal anesthesia injected intraperitoneally (0.6 cc/kg). The temporal bone was removed and the dura incised over the inferior lateral surface of the temporal lobe. In the AM animals, the zygoma was removed in order to expose the pole; in the IT operates, anastomotic veins were coagulated and severed at their entrance into the lateral sinus to permit exposure of the ventral surface. Neural tissue was removed by subpial aspiration with a small-gauge sucker. Sham operates were divided equally into those receiving the AM and IT procedures. The sham operations were identical to the others, except that no neural tissue was removed.

### *Anatomical Procedures*

Following experimentation, all *S*s were sacrificed, their brains embedded in celloidin, and the blocks serially sectioned at 25 mμ. Every twentieth section was stained with aniline thionin, and every fourth stained section was used to make an orthogonal projection onto graph paper. Sections were examined microscopically for evidence of damage.

Reconstructions of the lesions of Groups I and II (see below) are shown in Figure 1. Reconstructions of Group III lesions, together with cross sections, are shown in Figure 2. Ventral views are shown for all animals. In addition, medial views are presented for the AM operates, and lateral views for the IT operates. The left side of each cross section corresponds to the *left* side of the ventral view.

In all the AM operates, the medial pole was destroyed. In three of the six animals, there was very slight sparing of the dorsal lateral portion of the amygdaloid complex bilaterally. In another animal, the slight sparing was restricted to the left amygdala (AM-95). In the remaining two animals (AM-82 and AM-94), the amygdala were completely destroyed. In all cases except AM-94, there was slight damage to the uncus on at least one side, but no damage to the body of Ammon's formation. It should be noted that AM-94 and AM-95 had relatively smaller lesions in terms of total mass of tissue removed.

In all the IT operates, the temporal pole, amygdala, and uncus were intact. In all IT operates, there was also slight damage to the subiculum (bilaterally except in IT-99), as well as slight damage to the anterior ventral portion of the body of Ammon's formation bilaterally in IT-60 and IT-76.

### *Subjects*

Eighteen immature, untamed monkeys (*Macaca mulatta*), approximately one to two years of age, were

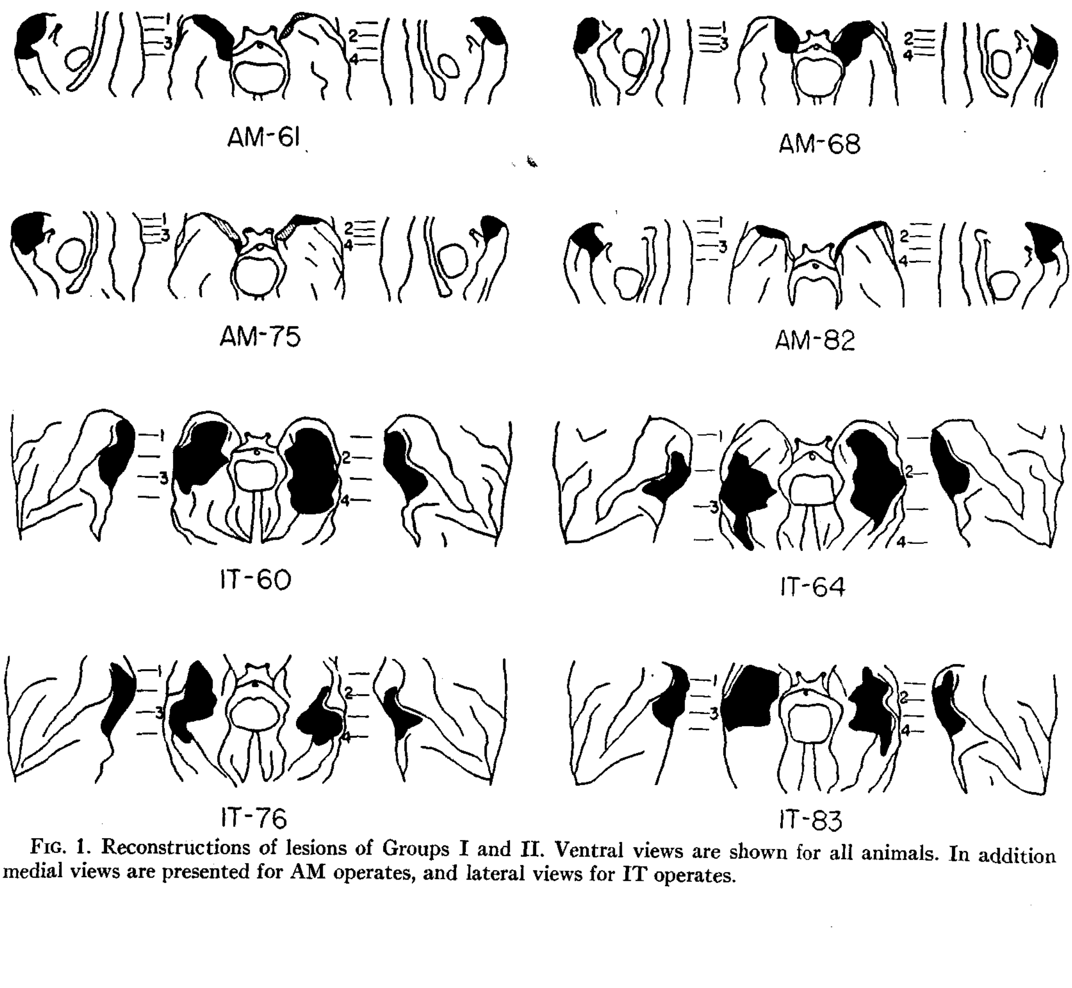


FIG. 1. Reconstructions of lesions of Groups I and II. Ventral views are shown for all animals. In addition medial views are presented for AM operates, and lateral views for IT operates.

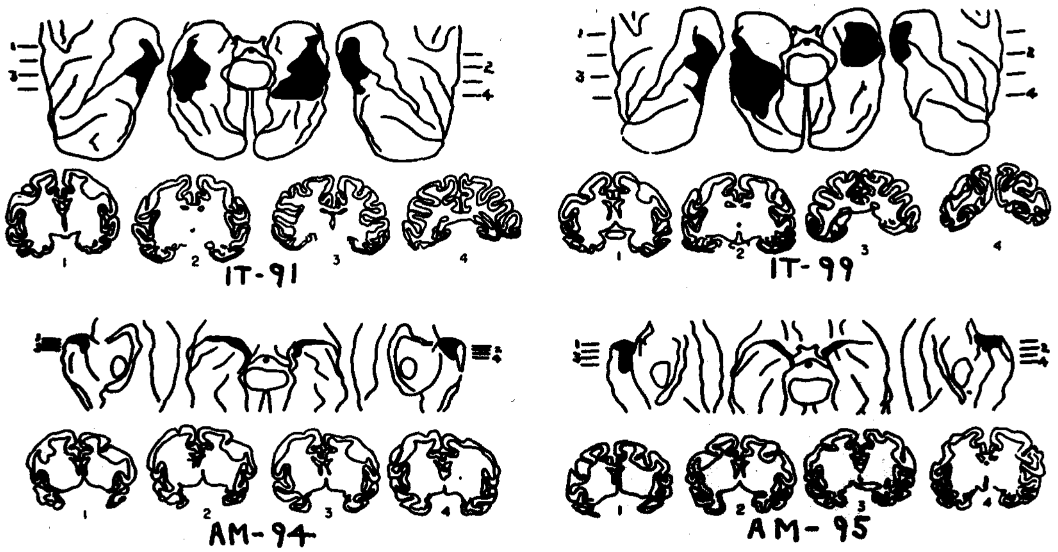


FIG. 2. Reconstructions and cross sections of lesions of Group III.

used. These animals ultimately consisted of 6 AM, 6 IT, and 6 S operates.

## *Apparatus*

*Conditioned avoidance.* A two-compartment shuttle box was used, each compartment measuring roughly 2 ft. by 2 ft. by 2 ft. The barrier separating the compartments was 12 in. high, and the opening measured 6 in. vertically and 18 in. horizontally. The floor of each compartment consisted of nine steel rods, ½ in. diameter, each of which could be electrically charged independently of the others. The walls and top of the cage, made of heavy wire screening, were wired as a unit and could also be electrically charged. A commutator device changed the polarity of each bar and the walls in a manner which made shock avoidance by straddling virtually impossible. The current flowing through the animal when shocked was about 1 ma., a.c., which reliably produced excited jumping but never tetanus.

Directly over each compartment was an electrical light fixture, appropriately shielded. A change from on to off was used as the conditioned stimulus. There was also a source of dim illumination some distance from the apparatus. The illumination in the center of each compartment with the compartment light on was 25.5 ft.-c.; with the compartment light off, 10 ft.-c.

The animal could be observed from an adjoining room through a one-way–vision screen. The conditioned stimulus (overhead light) could be controlled either manually or automatically. The shock circuit was operated manually. The *E* operated a foot switch which recorded, on an Esterline-Angus recorder, the position of the animal with respect to the CS. In addition, the duration and position (left or right compartment) of the CS were automatically recorded.

*Conditioned depression.* The apparatus consisted of a panel-pressing cage, 20 in. by 20 in. by 20 in., placed in a large soundproofed room. A force of 94 gm. on the panel through a distance of 2 mm. closed a micro switch. A food dish was available through an aperture below the panel. A 40-w. overhead light provided general illumination. Simultaneously with the delivery of a food pellet, the overhead light was extinguished and a 7-w. bulb illuminated the food dish for a period of 4 sec.

Food was delivered by an Anger pellet dispenser. Pellets were specially prepared from Lab Chow and pulverized peanut: they were .130 in. thick, .156 in. in diameter, and weighed .047 gm. on the average.[2]

Immediately over the cage was fixed an automobile horn, powered by a 10-v. battery charger. The intensity of the sound produced by the horn was between 95 and 100 db. In addition, a buzzer was fixed near the horn, which could produce a noise 2 db. above the noise level of the room. There was a constant masking noise of roughly 35 db.

Shock could be delivered to an animal through a low-resistance swivel chain attached to an aluminum collar around the animal's neck. The metal cage constituted the ground. The shock generator was an induction coil transformer, with an input of 1½ v. or 3 v., d.c., and with a turns ratio of 5000/1. The shock reliably produced a jerky, excited response.

## *Training and Surgical Program*

This information is contained in Table 1. Note that in the conditioned avoidance and conditioned depression situations, one of the groups received all training following operation, while the other received *acquisition prior* to operation and *extinction following* operation.

## *Testing Procedures*

*General observations.* Observations were made before and after operation of the animals' responses to human

[2] Formula available from P. J. Noyes Co., Lancaster, N. H.

TABLE 1
Training and Surgical Program

| Group I | Group II | Group III |
|---|---|---|
| Surgery | | |
| 8 days rest | | |
| Preconditioning | Preconditioning | |
| Avoidance acquisition (shock) | Avoidance acquisition (shock) | |
| | 2–3 days rest | |
| | Surgery | |
| | 8 days rest | |
| Avoidance extinction | Avoidance extinction | |
| | Reconditioning (shock) | |
| | Avoidance acquisition (man) | |
| Panel-press training | | Panel-press training |
| Conditioned depression acquisition (noise) | | Conditioned depression acquisition (shock) |
| | | 2–3 days rest |
| | | Surgery |
| Other procedures (not reported here) | | 8 days rest |
| | | Continued depression extinction |
| | | Depression acquisition (man) |
| Extinction of panel-pressing | | Extinction of panel-pressing |

observers, and to sticks and leather gloves, which had been associated with strongly aversive aspects of laboratory handling.

*Avoidance preconditioning, conditioning, and extinction.* On the day preceding the beginning of conditioning, each animal was put in the shuttle box for a 25-min. period. The door between the compartments was open, permitting movement back and forth. One compartment was lighted, the other unlighted. Every 30 sec., the lighting arrangement was reversed; thus in 25 min. there were 50 alternations of the lighting pattern. The total number of jumps from one compartment to the other was computed, as well as the total length of time spent in each compartment.

In the acquisition procedure, also, the door between compartments remained open; similarly, every 30 sec. there was an alternation of the lighting arrangement. Four seconds after an alternation, shock was applied if the animal was in the *dark* compartment. In addition, an animal was shocked for retracing into the dark compartment. The dark compartment was selected for shock because animals had a slight preference for it during preconditioning. Fifty trials were given daily, until an animal attained criterion by receiving less than six total shocks in a daily session. (It was found in preliminary work that the conventional *closed-barrier* shuttle box was not appropriate for our monkeys. With many animals, merely raising the door between compartments aperiodically was accompanied, after a hundred occasions or so, by jumps of short latencies through the door.)

Extinction differed from acquisition only in the omission of shock. Each animal was run in extinction for ten days.

*Panel-pressing training, conditioned depression acquisition, and extinction.* Animals were fed a constant diet prior to panel-pressing training, and then deprived equally. By the time conditioned depression acquisition began, each was receiving four pieces of Purina Lab Chow, six peanuts, and a quarter of an orange daily. Panel-pressing training was accomplished by conventional "shaping-up" techniques, until each animal stabilized on a 1-min. variable-interval schedule of reward. The average rate of response on this schedule was about 550 responses/hour.

Each conditioned depression session lasted 30 min. Prior to the introduction of electric shock or loud noise, the buzzer was sounded once during each daily session for 1 min. until the initial depression to it had adapted away, i.e., until there was a negative rate index of .15 or less on two successive buzzer presentations. Depression in this and all other instances was expressed by an index commonly used by a number of investigators:

$$\text{Rate Index of Depression} = \frac{C - NC}{C + NC}$$

where $NC$ is the number of responses during a *noncritical* interval (the 1-min. period prior to the buzzer sounding) and $C$ is the number of responses during a *critical* interval (the 1-min. buzzer sounding period).

To establish conditioned depression, Group I was given 21 sessions in which the 1-min. buzzer was terminated by the sounding of the automobile horn for 5 sec. The time during the 30-min. panel-pressing session was varied according to a predetermined schedule to avoid a temporal discrimination. Group III, which had not had the prior avoidance training, did not depress to the loud horn, and therefore was switched to electric shock. Each animal was run daily until it had a rate index of at least −.67 on four out of any five daily sessions, including the first and fifth of these sessions. For three animals (Group A) the shock input was set at 1½ v., and each shock consisted of two brief pulses; the other group (Group B) had an input of 3 v., with four pulses.

The extinction procedure consisted of ten daily sessions in which the buzzer was presented without being followed by the horn or by shock.

*Experimental measures of tameness.* In order to obtain an experimental measure of tameness, Group II was employed in a procedure identical to the acquisition of conditioned avoidance, except that the appearance of the $E$ was substituted for the electric shock if the animal was in a compartment 4 sec. after it had been darkened. This was accomplished by fitting an opaque screen against one side of the shuttle box, with a small centrally placed one-way–vision window, behind which stood *E*. A metronome, beating four times a second, provided the timing cue for *E*. At the appropriate moment for "shock," *E* would lean out beyond the edge of the screen, rendering his head visible. As far as possible, a constant facial expression was maintained, with visual fixation directed at the barrier separating the two compartments. Each animal was given 30 trials daily, for five days. As in the shock procedure, there was a preconditioning session to ensure that the mere presence of the opaque screen (with *E* behind it) did not produce "spontaneous recovery" of jumping to the CS.

Likewise, in the panel-pressing situation, *E* entered the experimental room and remained at a distance of 3 ft. from the experimental cage from the tenth to the fifteenth minutes of the session. No other conditioning stimuli were presented. During this time, *E*'s visual fixation was on the panel. The animal's rate during the preceding 5 min. was used in computing the rate index.

*Extinction of panel-pressing*. All contingencies produced by the 1-min. variable-interval schedule were kept the same except for the operation of the food magazine. Secondary reinforcement was still available in the turning off of the overhead light and simultaneous illumination of the food dish. The experimental session began with a 10-min. period in which food reward was presented as usual. Then extinction was carried out for 2 hr.

Group I had just completed another food deprivation experiment not reported here and was probably hungrier than Group III. For this reason, the results for the two groups will be analyzed separately.

## RESULTS

### *General Observations*

Postoperatively there was an immediate and unmistakable difference in appearance and behavior between AM operates and controls. The AM animals permitted petting and handling without visible excitement, or even approached and reached for observers. On the other hand, control operates continued to display their fear of and hostility toward humans by running to the farthest corner of the cage, frequently urinating and defecating, grimacing, and screeching. The AM operates were also altered in their reactions to sticks and gloves, handling and chewing them without hesitation. Controls showed the same violent behavior toward these objects as they had preoperatively.

During the first two or three postoperative days, the posture of the AM operates was hunched, their behavior sluggish; the slang designation "amygdaloid hangover" emerged as a summary description of this period. But even in this groggy state, the general tendency was approach rather than avoidance of observers. There was, in addition, sustained piloerection during the "hangover" period, which then subsided. There was no difficulty in initiating eating in the AM operates, with the notable exception of AM-66. After refusing food for 48 hr., *S* "learned to eat" again by having a finger of a glove on which banana was smeared forced into its mouth, after which it began vigorously chewing on the glove and soon consumed the rest of the banana, though it would not accept other types of food. The following day, this procedure was successfully repeated, using an orange. The day after, *S* was eating normally.

The excessive oral examination of objects reported by Klüver and Bucy (for temporal lobectomized animals) was also observed in the present group of AM operates, but diminished after a week to ten days. In some cases, food ingestion was quite indiscriminate, and included feces and horse meat.

Hypersexuality, reported by other investigators (7, 14) was never observed, but this may have been because of the sexual immaturity of all experimental animals and their isolation in single cages during the course of experimentation.

### *Postoperative Acquisition of Conditioned Avoidance and Depression*

There was a tendency for AM operates to take somewhat longer to acquire both of these behavior patterns when compared with the sham operates. Thus, in Group I, the two AM animals required 350 and 250 trials (including criterion trials) to learn conditioned avoidance, while the S operates required 200 and 150 trials. Again, in the acquisition of conditioned depression, the two AM operates required eight and nine days to depress consistently, while the S operates required two and three days. In both these problems, however, one of the IT operates deviated from the sham operate level. In avoidance training, IT-76 required 300 trials and IT-83 required 150. In depression training, IT-83 never consistently depressed but oscillated from complete depression on some occasions to complete lack of it on others, while IT-76 required three days to reach a consistently low level. Hence, with the small number of animals available for analysis, no

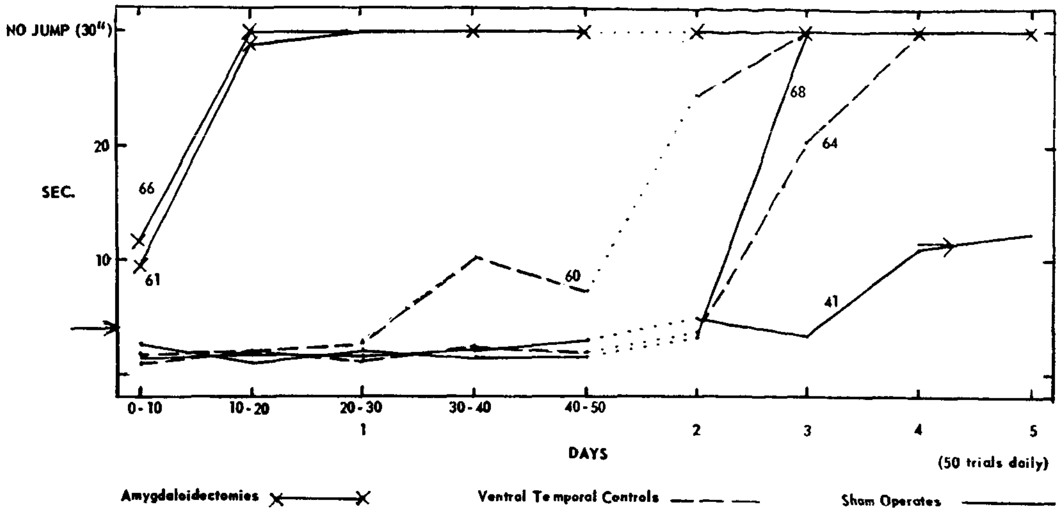


FIG. 3. Extinction of conditioned avoidance.

definite statement can be made regarding dissociation of the groups.

In the conditioned avoidance extinction procedure, no differences were obtained among the Group I animals.

### *Extinction of Conditioned Avoidance and Depression Acquired Preoperatively*

The AM operates extinguished considerably more rapidly than either of the two other groups in the shock avoidance situation. Figure 3 shows the extinction curves, plotted in terms of median latencies. Since the greatest change occurred within the 50 trials of the first day, these trials have been broken up in the graph into five groups of 10 trials each. From the second to the fifth days, daily trials have been treated as a single block. A plot in terms of percentage of time spent in the formerly shocked compartment yields a similar picture. Figure 3 is useful in showing that the AM operates *did* jump within the first 10 trials, and hence this phenomenon was truly more rapid extinction rather than amnesia.

Large savings were shown by all animals in the avoidance reconditioning procedure, with no significant differences among the groups.

Figure 4 is a plot of the first ten days of extinction of conditioned depression, with the two training subgroups (based on strength and number of shock pulses) shown separately. In both groups the AM animals tended to recover more rapidly than either of the controls, although this difference is not as marked as in the avoidance experiment.

The bar-pressing situation provided an important additional datum, i.e., the rate of response during each session, omitting the 1-min. buzzer intervals and the 1-min. period immediately succeeding. In terms of percentage change of response rate postoperatively from a ten-day average computed for each animal preoperatively, all animals pressed more slowly following operation. There was, however, no suggestion of a difference with respect to lesion.

### *Avoidance of and Depression with Respect to Man*

The experimental measures of tameness bore out the gross observations that the AM operates were tamer than controls. Figure 5 plots the proportion of each day's 30 trials in which each animal avoided *E* (i.e., jumped with a latency of less than 4 sec. following the CS). With the exception of a few trials on the first day for one AM animal, there were no avoidance responses for this group. Control animals were quite variable, but all displayed a significant degree of avoidance throughout the five-day period. On the remainder of the trials, the non-avoidance trials, there was an equally clear difference between the AM and control groups. The former showed very few escape responses, while the latter demonstrated a very high proportion of such responses.

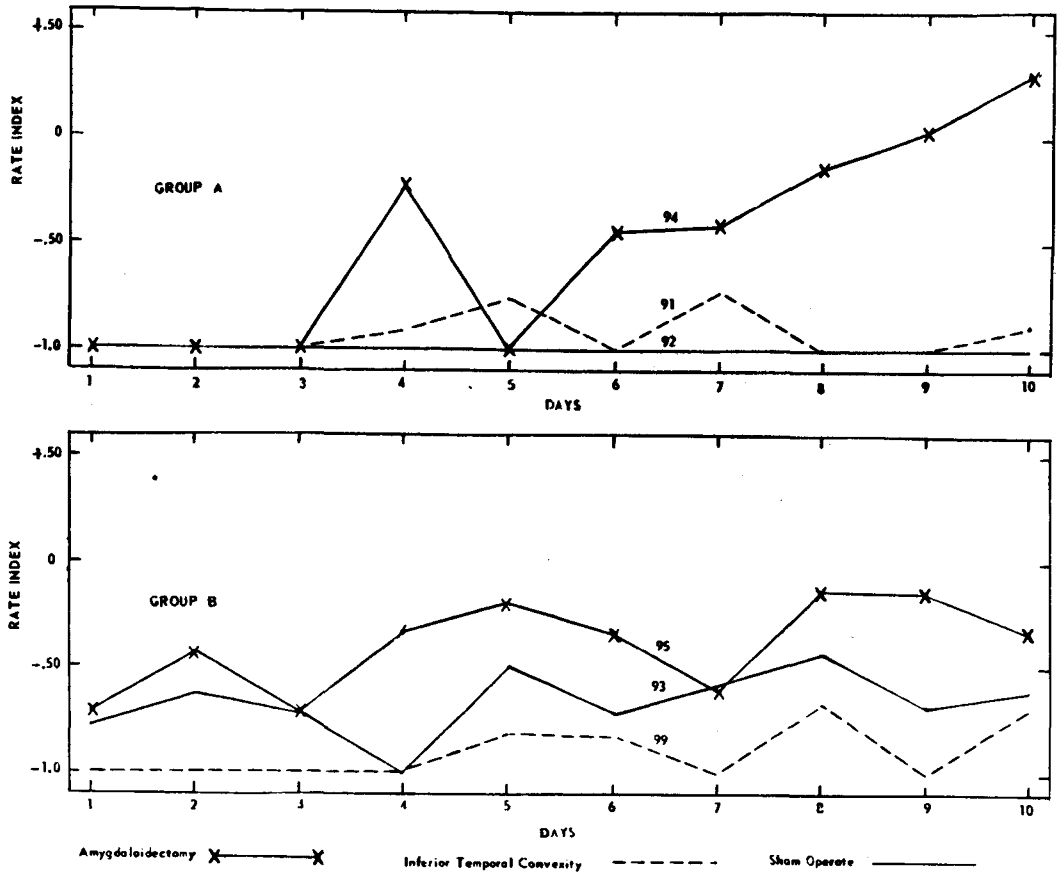


FIG. 4. Extinction of conditioned depression.

Similarly, in the depression experiment, the 5-min. appearance of *E* made less difference to the panel-pressing of AM operates than it did to others. The rate indices of the two AM operates were +.04 and −.24; of the IT operates, −.54 and −.97; and of the S operates, −.83 and −1.00.

*Extinction of Panel-Pressing*

In considering the extinction data, one measure which would have generality would be the fitting of positive growth functions to the cumulative records, solving for the rate of growth factor, $-k$. A less laborious expedient has been adopted here. On the basis of the animal's performance during the 10 min. of rewarded panel-pressing, an "expected" value of the total number of responses was calculated which would have been made in a 2-hr. period had the original rate been sustained. Then the observed number of responses was expressed as a percentage of the expected value.

The results of such an analysis are shown in Table 2. The two groups of animals differed in the average percentage values obtained, perhaps as a result of the condition discussed above. In spite of this, within each group the AM operates had higher percentage values than controls, i.e., made relatively more responses than controls. The last column attempts to make the two groups more comparable by listing the percentages relative to the two sham operates in each group. (One IT animal was not run in this experiment.)

DISCUSSION

In both the avoidance and the depression situations: (*a*) man was less of a disturbing or aversive factor to the AM operates than to controls; (*b*) the AM operates had a slower

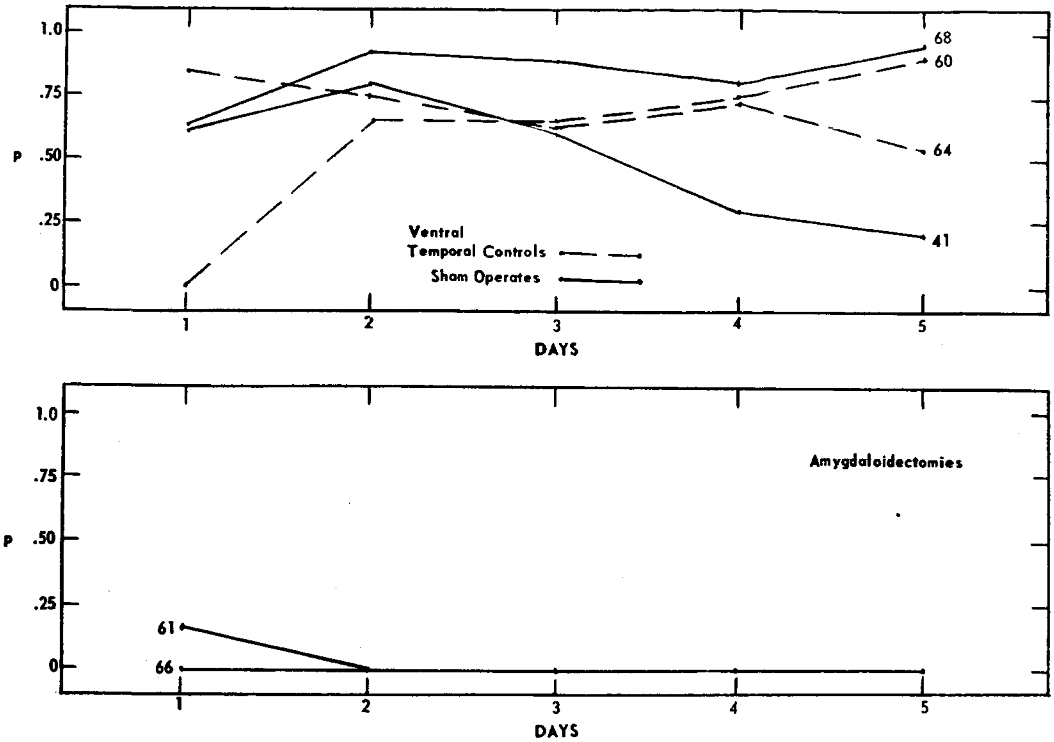


FIG. 5. Proportions of avoidance responses to experimenter.

rate of acquisition than sham operates, but in both situations one IT operate deviated from the sham operate level; and (*c*) the AM operates had a faster rate of extinction for conditioned avoidance and depressive behavior established preoperatively.

Consideration must be given to other behavioral relationships which may have been affected by the lesion, producing the above results only secondarily. One of the most pertinent is that of activity level, since amygdalectomized rats have been reported to show marked reductions in activity wheel rate (1), and since one might predict the present results from a lowered activity level. Two investigations employing monkeys, however, have failed to find activity changes in temporal lobe operates (3, 6). In the present study, since the AM operates did not differ from controls in their over-all rate of panel-pressing, the more rapid extinction of conditioned depression cannot be explained simply in terms of an activity change, since panel-pressing was the specific activity against which the depression was measured. In the avoidance situation, no such base line was available, but analysis of the number of jumps between compartments in the preconditioning session for Group I fails to reveal any difference between AM operates and other operates.

TABLE 2
Extinction of Panel-Pressing

| Group | Animal No. | $\frac{\text{Observed}}{\text{Expected}} \times 100$ | Relative to Sham Operation Average |
|---|---|---|---|
| I | AM-75 | 80.5 | 1.71 |
| | AM-82 | 74.4 | 1.58 |
| | IT-83 | 43.0 | .91 |
| | IT-76 | 62.4 | 1.33 |
| | S-78 | 44.6 | (1.00) |
| | S-77 | 49.4 | |
| III | AM-95 | 47.4 | 2.05 |
| | AM-94 | 38.1 | 1.65 |
| | IT-99 | 16.2 | .70 |
| | S-93 | 23.7 | (1.00) |
| | S-92 | 22.5 | |

Similarly, the fact that AM operates were slower than controls in their rate of panel-pressing extinction argues against an explanation in terms of "decreased vigilance" or in terms of a tendency for all classes of behavior to extinguish more rapidly. Inasmuch as the food extinction procedure normally elicits many "emotional" responses, which in turn depress rate of response, it can be argued that the slower rate of extinction by AM operates followed from their decreased response to "anxiety-producing" situations.

Most of the AM and IT operates in the present series were subjected to tests of visual discrimination (unpublished study by Mishkin and Pribram). On the whole, they confirmed previous findings that IT operates are, and AM operates are not, impaired in such discriminations (see introduction). The impairment of the IT operates, it should be pointed out, should not have interfered seriously with so simple a visual discrimination as required in the avoidance situation (8, 9), and even if it had, what differences were obtained should warrant even greater confidence. Even given the possibility of confounding of relationships, the present study, taken in conjunction with studies of IT lesions, supports the conclusion that the effects on behavior of removing the AM and IT areas are dissociable.

No claim is made here that amygdalectomy is the only type of cerebral lesion which produces rapid postoperative extinction. Other results, in fact, suggest that a large system may produce similar results (unpublished study by Pribram and the author). Even within the medial temporal region, there is no certainty that damage to the amygdaloid complex, as such, is essential. Two investigators have produced very tame monkeys by lesions which were near, but outside, the main body of the amygdaloid complex (16, 17). Enlarging the size of the medial temporal lesion to include anterior insula and posterior orbital cortex increases the severity of the behavioral changes (unpublished data), but there are not sufficient data to decide whether the relationship is a simple function of mass within this complex, or whether a focus exists. It should be noted, in this connection, that the smaller difference in rate of extinction between AM and other operates in the depression situation as compared with the avoidance situation may be related to the smaller mass of the AM lesions in the former instance.

Reference has already been made to discrepancies produced by previous investigations. Until more evidence is available regarding anatomical limits of lesions, speculative reconciliation is perhaps fruitless. This study has a special point to make, however, with regard to a possible source of discrepancies, in that AM operates were found to extinguish more rapidly avoidance responses established preoperatively. If man is at least partially a conditioned aversive stimulus to the monkey, then postoperative tameness may be the result of rapid extinction of avoidance responses to man. On the other hand, no severe loss either in retention or in the ability to acquire new avoidance learning was found. These facts suggest that particular aspects of postoperative treatment can be of great importance in producing tameness, on the one hand, if previous avoidance responses are permitted to extinguish, or increased fear, on the other, if additional aversive stimulation is introduced. Procedures, therefore, such as "blowing on the face" (2, p. 392) or "threatening the animals, cuffing them about the head, pinching their ears or paws, and suspending them in mid-air by their tails or one lower extremity" (14, p. 643), may be important independent variables. We have found, in a preliminary test of this general notion, which also has support from an analysis of the effects of aggressiveness of cagemates on operated animals (13), that an AM animal treated gently and in a pet-like fashion after operation remained tame for several months, whereas one treated indiscriminately like a normal laboratory animal was grossly indistinguishable from a normal within a period of six weeks.

Brady, *et al.* (4) have reported that amygdalectomized cats acquire avoidance conditioning more slowly than normal controls; AM cats were not impaired in retention of avoidance behavior. Brady's tempting interpretation that only the acquisition, and not the maintenance, of avoidance behavior is affected by amygdala lesions is not upheld by more recent data, at least in monkeys (18). The present study adds to Brady's evidence, however, that AM operates are altered in their adaptation to emotional stimuli. The question still remains, though, whether it is most economical, descriptively and conceptually, to subsume all the effects of amygdalectomy under the heading of emotional behavior. One of the "dietary changes" sometimes noted following amygdala lesions in monkeys is the ingestion of feces (12). It is doubtful if this could be accounted for simply in terms of decreased fear. Again, the hypersexual behavior noted by some researchers (7, 14) seems too extreme to be normal, unfettered libido. One vague explanation which could account for all these phenomena will be advanced briefly. The effect of amygdalectomy, it is suggested, is to make it difficult for reinforcing stimuli, whether positive or negative, to become established or to be recognized as such. Sometimes the difficulty is seen in overgeneralization, as when an animal attempts to ingest any object within reach, and sometimes it is in the lack of appropriate response to any stimulus, as when an animal must be "taught to eat." According to this notion, AM operates should not be hyperphagic or hypersexual, but *indiscriminately* phagic and sexual. It is not assumed that the behavioral alteration is a static one; immediate postoperative experience would be of great importance in establishing the particular repertoire of primary and secondary reinforcers. (This idea has features in common with the unpublished suggestion of Olds that amygdalectomy produces lack of discrimination of "motivationally relevant stimuli".)

There is the traditional difficulty in precisely defining "reinforcing stimuli," but for present purposes the definition need be only descriptive. No implication is intended that stimuli normally considered to be "primary reinforcers" are not loaded with secondary or learned components; in fact, quite the contrary. Assuming the suggestion that AM operates have trouble with the identification of reinforcers is descriptively adequate, then further questions arise: Is the difficulty due to (*a*) sensory impairment, (*b*) a faulty bodily response to the stimuli, or (*c*) a faulty relating of the bodily response to the external stimuli? These questions point the way for subsequent analytical research. Recent evidence tends to rule out sensory impairment (8, 9), but suggests a positive answer to the second question, in that certain metabolic processes seem disturbed (personal communication with W. A. Wilson, Jr.). Much more evidence will be required before the fruitfulness of the present conception can be evaluated.


## SUMMARY

The performance of monkeys sustaining experimental lesions of the amygdala and medial temporal pole, or control lesions in the inferior temporal convexity or control sham operations, was studied grossly and with respect to the acquisition and extinction of conditioned avoidance and conditioned depression behavior. The following results were obtained:

1. In gross behavior, a marked increase in tameness and a weakening or disappearance of fear responses to previously aversive stimuli by amygdala animals.
2. A lower level for amygdala animals of avoidance and depression with respect to man as measured experimentally.
3. More rapid extinction by amygdala animals of conditioned avoidance and conditioned depression, when these behaviors had been established preoperatively.
4. A slower rate of acquisition of these behaviors by amygdala operates when compared with sham operates, but not when compared with inferior temporal operates.
5. No differences among groups in retention of avoidance behavior.

Various possibilities that other behavioral changes may have secondarily produced the results are discussed. Evidence tends to rule out activity level changes, "decreased vigilance," or impairment in visual discrimination in amygdala animals. It is suggested that the effect of amygdalectomy is to make it difficult for animals to identify reinforcing stimuli.


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