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Bilateral amygdalectomy of monkeys is shown to interfere with transfer of training in the Klüver stimulus equivalence situation. Further, failure to make "equivalent responses" reflects some process other than that involved in stimulus generalization because differential removals of temporal lobe tissue result in "double dissociation" of the interference with transfer and with stimulus generalization. Amygdalectomy alters primarily transfer of training; inferotemporal cortical resections alter primarily stimulus generalization and discrimination. The nature of this process, basic to transfer of training, remains to be investigated.

The present line of investigation began with the observation that amygdalectomized *Ss*, in contrast to controls, run alternately under conditions of reinforcement and extinction responded to each set of reinforcing events as if the extinction runs had not been interposed (Schwartzbaum, 1960b). Efforts were therefore directed to test whether this effect of amygdalectomy was limited to situations in which the role of reinforcers is crucial, or whether it occurred more generally, involving other properties of stimulus events. Changing light conditions did not produce habituation of the amount of locomotor activity in amygdalectomized monkeys (Schwartzbaum, Wilson, & Morrissette, 1961). Transposition of responses in a brightness discrimination task was also found defective (Schwartzbaum & Pribram, 1960). Thus it proved unlikely that bilateral amygdalectomy affected only behavior under the immediate control of reinforcers. Because of its theoretical importance (Pribram, 1960, 1963, 1964) this effect of amygdalectomy on transfer of training merited additional investigation.

PROCEDURES

Subjects

Eighteen naive immature rhesus monkeys served as *Ss*. After the initial training procedures four of the monkeys received bilateral single stage ablations of the amygdala; the remaining *Ss* served as controls. Of the controls, six received small bilateral removals of cortex of the inferior temporal gyrus; eight were not subject to surgery.

The surgical and histological procedures carried out were the same as those described in Schwartzbaum (1960a). The inferotemporal cortical lesions were made by the same approach, a limited area of ventral temporal cortex anterior to the vein of Labbé was removed. Reconstructions of the lesions are shown in Figures 1 and 2.

Apparatus

A modified Wisconsin General Testing Apparatus (Schwartzbaum & Pribram, 1960) containing a response panel painted black was used. Two doors, measuring 7.5 × 7.5 cm. and set 17.5 cm. apart at their centers, concealed foodwells which could be reached by pushing inward on a hinged door. Reward was half a peanut. The interchangeable doors each displayed one square white plastic (Contact) cutout. Pairs of squares differing in area by the ratio of 1.5:1 were used.

Training stimuli measured 8.0 × 8.0 cm. vs. 6.5 × 6.5 cm., whereas the equivalence stimuli measured 5.7 × 5.7 cm. vs. 4.6 × 4.6 cm. The areas of the equivalence test pair (32 $cm.^2$ vs. 21 $cm.^2$) were one-half the areas of the training pair (64 $cm.^2$ vs. 42 $cm.^2$).

The lighting was arranged to allow the 40-w. fluorescent light over the stimulus doors to switch on as the two house lights mounted on the sides of the animal section were shut off. A manually operated one-way vision screen separated the response panel and its light from the animal section.

Training Procedure

Preoperative. All *Ss* were trained to choose the larger (64 $cm.^2$) square of the training pair. Noncorrective technique (30 trials daily for 6 of 7 days a week) was used to a criterion of 90% correct in 100 consecutive trials. The right-left position of the positive stimulus was varied according to a modified Gellermann schedule. The cues were lighted for a period of 3 sec. before the screen was raised on each trial. This procedure was designed to minimize possible indiscriminate impetuous approach reactions. Retention was tested after 7 days by the same technique (30 trials a day for 3 days). The last 10 retention trials were given on the fourth day as described below. Equivalence tests followed the final 10 training trials with the equivalence stimuli presented for 20 trials with reward for either response.

Postoperative. Following a 2-week recovery period all *Ss* were tested for retention of the discrimination. Animals with less than 90% retention in 100 trials (two inferotemporally operated *Ss*) were retrained to 90% criterion. Equivalence trials were then readministered as preoperatively.

Performance was expressed as the number of equivalent responses and calculated as responses to the same stimulus minus 10. This value gives the number of responses above chance performance. Thus an *S* who chose the same stimulus all 20 times scored 10 equivalent responses, the maximum, whereas an *S* who chose each stimulus 10 times scored 0 equivalent responses, or chance.

Results

No gross behavioral differences between animals were noted in the test situation. However, the home cage behavior of the amygdalectomized *Ss* was strikingly different from the normals

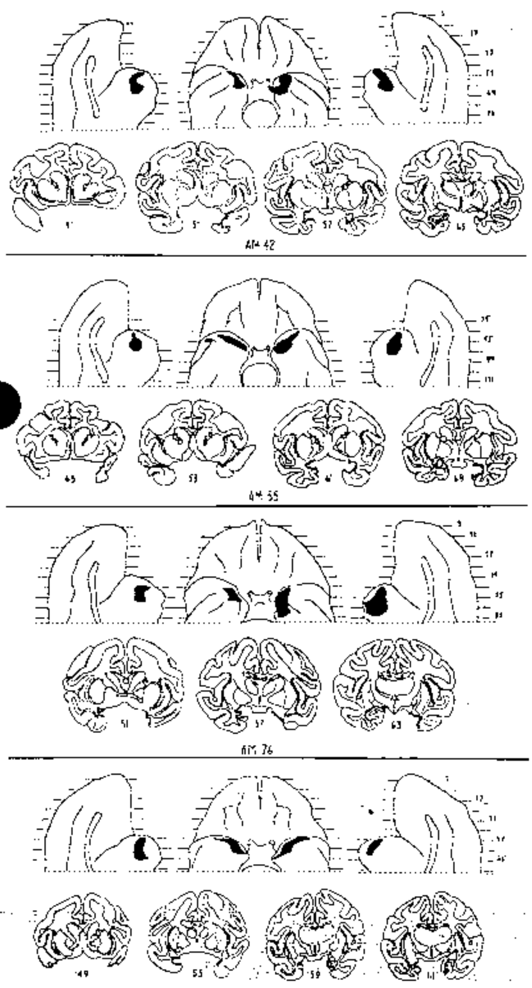

Fig. 1. Reconstructions of amygdala lesions. (Dashed areas denote spared tags of amygdala. Dark areas denote ablations.)

and the inferotemporal operatees. This behavior was quite similar to that described by Weiskrantz (1956) and by Fulton, Pribram, Stevenson, and Wall (1949) and included excessive tameness, indiscriminate approach to observers, frequent inappropriate mounting behavior, and persistence of putting lighted matches in their mouths despite burning of whiskers.

Initial training on the discrimination required 170–220 trials ($M = 205$) by the amygdalectomized group (AM), 205–610 trials ($M = 387.6$) by the unoperated monkeys (N), and 193–381 trials ($M = 256.6$) by the inferotemporally operated *Ss* (IT). Preoperative retention was above 90% in 100 trials for all *Ss*.

Individual scores for trials to criterion and errors to criterion showed low correlation with the equivalence scores before surgery.[1]

In postoperative retention two inferotemporally operated *Ss* required 40 and 50 additional trials each to reach criterion.

Equivalence performance is summarized in Table 1. All unoperated *Ss* increased their scores except one who continued at the preoperative level. The group (N) average increase was 2.75 equivalent responses. On the other hand, all amygdalectomized *Ss* scored lower postoperatively, with an average change of −5.25 equavalent responses. The performance of the inferotemporally operated control groups was less clearly demarcated (group mean change, −0.83). Two of these *Ss* increased and four decreased their scores slightly. Of the two inferotemporals who had slight difficulty with discrimination retention, one decreased his equivalence response score from 4 to 2; the other increased from 1 to 2. (Differences between the group equivalence scores are significant at better than the .02 level using a *t* test.)

Expressed in terms of percentage of preoperative performance the same group differences emerge. Normal monkeys gave 64.7% more equivalent responses, while the amygdalectomized group gave 84% fewer. The inferotemporally operated monkeys responded 19.9% less than preoperatively.

Discussion

Amygdalectomy markedly interferes with the transfer of training in the stimulus equivalence situation. The impairment is not due to defective visual discrimination as originally shown by Pribram and Bagshaw (1953) and confirmed in

[1] Variability in the initial equivalence scores was probably related to the size differential chosen and would have been less at 2:1 as used by Klüver (1933). However, this variation was not significant across the three groups according to a *t* test.

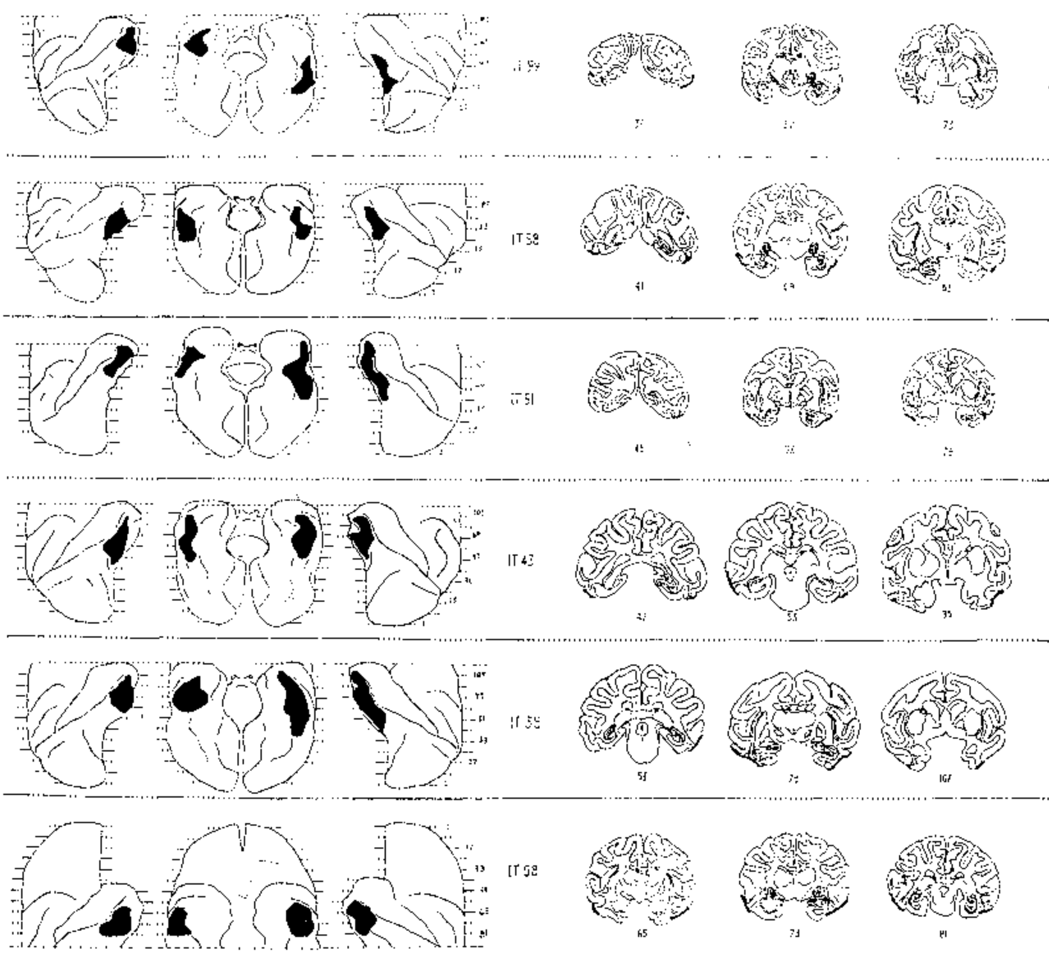

FIG. 2. Reconstructions of inferotemporal lesions. (Dark areas denote ablations.)

this study, since the original task performance was retained postoperatively. Nor is it likely due to a change in stimulus generalization, since in other situations, generalization was shown to be intact in these operatees (Hearst & Pribram, 1964). What then, can account for the results?

Several recent publications have been concerned with the problem of brain function in stimulus generalization and equivalence performance (e.g., Thompson, 1962). These have dealt with the effects of isocortical resections and have shown that these procedures produce generalization curves flattened relative to those of controls (Butter & Mishkin, 1963). In contrast, the performance of stimulus equivalence tasks was unaffected (Hara & Warren, 1961a, 1961b).[2]

The results obtained from our small inferotemporal lesions are of interest in this regard. These *Ss* failed as a group to display the increase in transfer shown by the normal group, yet their equivalence scores did not fall as did those of the amygdalectomized *Ss*. Inferotemporal lesions do drastically disrupt discrimination (Pribram & Mishkin, 1955) and markedly increase stimulus generalization (Butter & Mishkin, 1963). This, despite the limited size of our lesions, would lead one to expect a decrease in equivalence scores. The failure to increase equivalence responses postoperatively is therefore amply accounted for by the hypothesis that inferotemporal resections impair the process of response selection. Could this same ex-

[2] There is a report by Hara and Warren that preoperatively established brightness preferences, tested by the method of equivalences, were disrupted by suprasylvian resections in cats. These authors also report, however, that the same technique, when used to test transfer of training, showed no discernible effect produced by the lesion (Hara & Warren, 1961a, 1961b).

TABLE 1
EQUIVALENT RESPONSE SCORES: NUMBER ABOVE CHANCE

S	Equivalent response scores		
	Preoperative	Postoperative	Change
Unoperated controls			
33	5	5	0
49	4	8	4
57	1	4	3
71	0	6	6
97	4	9	5
115	7	9	2
116	7	8	1
118	6	7	1
M	4.25	7.00	2.75
Amygdalectomized *Ss*			
42	9	1	-8
55	6	2	−4
76	8	1	7
117	2	0	−2
M	6.25	1.00	−5.25
Inferotemporal lesioned *Ss*			
38	4	2	2
43	3	1	−2
58	5	3	−2
51	1	2	1
98	4	2	−2
99	8	10	2
M	4.16	3.33	0.83

planation be invoked to account for the effects of amygdalectomy on equivalence and transposition?

Patently, as the evidence stands at the moment, the answer is no. Discrimination and generalization are little, if at all, affected by amygdalectomy, yet equivalence performance is drastically disrupted, transfer of training impaired. The suggestion from this "double dissociation" of lesion effects is that tests of transfer of training which use the method of stimulus equivalence and of transposition are able to delineate a process other than the one reflected in the performance of stimulus generalization and discrimination tasks. The nature of this transfer of training process remains to be specified.

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