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Reprinted from:
JOURNAL OF COMPARATIVE AND PHYSIOLOGICAL PSYCHOLOGY
Vol. 53, No. 4, 1960

Journal of Comparative and Physiological Psychology
1960, Vol. 53, No. 4, 396-399

THE EFFECTS OF AMYGDALECTOMY IN MONKEYS ON TRANSPOSITION ALONG A BRIGHTNESS CONTINUUM[1]

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In the previous report (Schwartzbaum, 1960), it was suggested that amygdalectomy might impair processes by which organisms interrelate different reinforcing events, i.e., respond to one set of reinforcing events in terms of some other set. The formulation implies that amygdalectomized animals fail to utilize their experience appropriately when they are confronted with "new" stimuli. If this supposition is correct, then one would expect the effects of the lesion to be more inclusive with respect to discriminative, as well as reinforcing, events. Conditions designed to maximize stimulus generalization and perhaps other forms of transfer of training should, as a first approximation, provide relatively sensitive indices of the impairment.

In the present experiment, a classical form of transposition problem was used to provide preliminary information about this assumption. Transposition represents essentially a form of generalization of response from one set of stimuli to another set ordered along some continuum. As such the problem satisfies the general conditions of the hypothesis.

Experiment 1

Method

Subjects. The *S*s were the same four amygdalectomized and four normal rhesus monkeys used in the experiments on free-operant behavior (Schwartzbaum, 1960). They had never been tested on conventional discrimination problems nor in the Wisconsin General Test Apparatus. A total of 10 to 15 months separated the start of the present experiment from the time of surgery. All animals were maintained on a daily diet of 8 to 10 Purina Lab Chow pellets and one-quarter of an orange, fed approximately 2 to 3 hr. after each test.

[1] The experiment was performed at the Institute of Living, Hartford, Connecticut, under a grant, No. M-546(C), from the U.S. Public Health Service, National Institutes of Mental Health. A report of the findings was presented at the 1959 meeting of the Eastern Psychological Association.

Apparatus. All tests were conducted in an air-conditioned, sound-insulated room with a modified Wisconsin General Test Apparatus fitted with a specially designed board, 18½ in. high and 24 in. long, that sloped toward the animal at an angle of 80° to the horizontal plane. The board contained two $4\frac{1}{16}$-in. square cutouts, spaced 3¾ in. apart and 6 in. above the base, which accommodated a pair of stimulus panels measuring 4 in. by 4 in. Each stimulus panel was mounted on a frame hinged at the top to the board. Thus, the panels could be swung open, allowing access to a small food cup located behind each one. The hinges were designed in such a way that the panels could be easily interchanged. Interposed between the board and the test cage was a movable one-way screen which shielded the board from the animal between trials. A distance of 6 in. separated the panels from the front of the test cage. Two 40-w. fluorescent fixtures mounted above and to the side of the test cage provided the illumination.

The stimuli consisted of three different shades of gray, each painted on a separate panel. The grays were prepared by appropriate mixture of a flat-black and a flat-white paint so as to appear spaced equally apart. When matched to the Munsell Neutral Value Scale, the following values were obtained: dark gray, N 3.5; medium gray, N 5.0; light gray, N 7.5. The board itself was finished in a flat black to provide a uniform contrasting background for the stimuli. Both the stimuli and the board were sprayed lightly with a transparent fixative to minimize fingerprints and other stains. Several panels were prepared with each of the grays so that a given panel was never used throughout a test session.

Procedure. Three days of preliminary training were required to accustom the animals to operating the panels and retrieving a food reward. In this training, the *S*s received 30 trials a day with two black panels. Either response was rewarded except when persistent position biases developed. In this event, the opposite response was rewarded selectively until the position habit was broken. The reward used throughout the experiment consisted of a half-peanut.

The formal testing began with a simultaneous form of gray discrimination. A dark-gray stimulus was paired with a medium-gray stimulus, with the medium gray as the positive stimulus for all animals. Thirty trials a day were given, using a noncorrection technique, in which the positions of the stimuli were varied in a balanced order in accordance with a Gellermann procedure. The trials were spaced approximately 25 sec. apart. Training continued to a criterion of at least 90% correct responses on each of two consecutive days.

The transposition tests followed the attainment of the criterion on the initial discrimination. The previously positive medium gray was now paired with a light-gray stimulus, and both were made positive. These conditions maximize the contribution of the prior training in the transposition performance. Six tests of transposition were carried out daily for two consecutive days during a continuation of the original discrimination procedure, making 12 such observations. The transposition stimuli appeared in counterbalanced position on every fifth trial of these sessions. Thus on 24 of the 30 trials, the dark-gray and medium-gray stimuli were presented, and on 6 trials, the medium-gray and light-gray stimuli appeared.

Results

The amygdalectomized monkeys tended to learn the brightness discrimination more slowly than did the normal monkeys, but the differences were small and not significant ($p > .05$, t test). They took an average of 172 trials (range of 150 to 240) and made 62 errors (range of 51 to 76) in reaching the criterion, exclusive of criterional performance. The normal animals averaged 112 trials (range of 90 to 150) and 48 errors (range of 34 to 69). Indeed, the differences obtained are exaggerated by the fact that two *S*s in the lesion group missed by one error attaining the criterion in 120 instead of 150 trials.

The transposition tests, on the other hand, strongly differentiated the two groups. As shown in Table 1, the normal animals transposed a median of 11 times of a possible 12, with little variability among animals. In contrast, three amygdalectomized animals closely approximated the chance level of performance, with perhaps a slight preference for the previously positive medium-gray stimulus. The fourth animal, which took longest to learn the original discrimination, exhibited a normal pattern of transposition.

TABLE 1

NUMBER OF TRANSPOSED RESPONSES MADE ON TRANSPOSITION TESTS

Day	Normals					Amygdalectomized				
	439	441	443	447	Mdn.	397	405	438	442	Mdn.
1	6	5	6	6		2	5	2	4	
2	5	5	5	6		3	6	2	2	
Total	11	10	11	12	11.0	5	11	4	6	5.5

EXPERIMENT 2

In order to define better the characteristics of the impaired transposition behavior, an additional test was performed. A sequential form of brightness discrimination was presented in which the medium-gray stimulus was paired "randomly" on different trials with either the dark-gray or the light-gray stimulus, but, in either event, the medium-gray stimulus remained positive. If the amygdalectomized animals had indeed shown a stronger response tendency toward the previously positive stimulus of the transposition pair, then they would be expected to do relatively well on this sequential discrimination. If, on the other hand, their transposition performance had simply reflected the transient effects of a novel stimulus, then there would be little reason to expect any group differences on a test that involved frequent repetitions of the experimental conditions. But in neither case would deleterious effects of the lesion be anticipated. The results obtained, however, tend to rule out both these possibilities.

Method

The same set of *S*s that completed the transposition experiment were tested on the sequential brightness discrimination. They were given 30 trials a day, using a noncorrection technique. Each pair of stimuli appeared in a randomized order on half the trials within a session. The criterion of learning was set at 90% correct responses on each of two consecutive days. The sequential discrimination was separated from the last transposition test by two additional days of training with the original pair of stimuli. All animals performed at criterional level in both of these sessions.

Results

Table 2 shows the number of trials required to meet the criterion on the sequential dis-

TABLE 2

PERFORMANCE ON SEQUENTIAL BRIGHTNESS DISCRIMINATION

Measure	Normals					Amygdalectomized				
	439	441	443	447	Mean	397	405	438	442	Mean
Trials to criterion[a]	60	30	30	30	38	150	330	210	120	202
% change from initial discrimination	−60	−67	−67	−75	−67	0	38	40	−20	14

[a] Excludes criterional trials.

crimination. The results demonstrate clearly a deficit in the performance of the amygdalectomized animals, although they were by no means unable to learn the problem. They required about five times as many trials to reach the criterion as did the normal animals (p = .028 by a two-tailed Mann-Whitney U test). But the rapidity with which the normal animals mastered the problem must also be noted.

A comparison of the performance on the sequential discrimination with that on the original discrimination, expressed as a percentage change in the number of trials to criterion (Table 2), provides a check for any initial group differences. Examination of the data shows that the groups still differed markedly on this measure of performance in the sequential discrimination (p = .028). The normal animals mastered the sequential discrimination in about two-thirds fewer trials than they took to learn the original discrimination. The animals with lesions required about the same number of trials as before.

It can be seen from Table 3 that the difficulty which the amygdalectomized animals encountered on the sequential brightness discrimination related almost exclusively to the presentations of the transposition pair of stimuli. About 95% of their total errors occurred with the transposition stimuli, accounting for virtually all the differences in performance between the groups on the sequential discrimination. Animal AM-405 showed this same form of impairment on the first 150 trials; then its performance pattern broke down into a more generally distributed deficit.

TABLE 3

DISTRIBUTION OF ERRORS ON SEQUENTIAL BRIGHTNESS DISCRIMINATION

Measure	Normals					Amygdalectomized				
	439	441	443	447	Mdn.	397	405	438	442	Mdn.
Total errors[a]	15	10	4	11	10.5	43	131 60	49	32	46.0
% total errors with transposition stimuli	87	100	100	91	95.5	95	76 90[b]	94	100	94.5

[a] Excludes criterional trials.

[b] Based on first 150 trials.

DISCUSSION

The transposition findings are consistent with the supposition that amygdalectomy impairs processes which are necessary for the generalization of a learned response. Given the training with a particular pair of stimuli, the animals with lesions did not respond normally to an overlapping set of stimuli on a brightness continuum. Indeed, their performance gave little evidence of the prior training. Whereas the normal animals markedly transposed their responses away from the previously positive stimulus, three of four amygdalectomized monkeys distributed their responses in what appeared to be a random manner.

Similarly, the difficulty which the amygdalectomized animals encountered on the sequential discrimination centered almost exclusively on those trials in which the transposition stimuli appeared. This again may reflect their failure to generalize appropriately. However, in this case the experimental design precludes any estimation of the actual amount of transfer involved. It is interesting that in spite of the "reversal" condition, i.e., the requirement for nontransposed responses, the normal monkeys learned the problem with such remarkable rapidity. This would suggest that the reversal conditions were of minor consequence. Nor would they seemingly account for the lesion impairment in view of the demonstrated ability of amygdalectomized monkeys on delayed-response and alternation types of problems (Mishkin & Pribram, unpublished data; Pribram & Bagshaw, 1953).

It should be emphasized that the term "generalization" is used here in strictly a descriptive sense. No claim is made about the mechanism that may underlie the disturbance in generalization. The complexities of transposition phenomena, as ably described in a recent review by Riley (1958), allow for many possibilities. Nor does the hypothesis advanced entail any assumptions about the nature of the stimuli or the psychological continuum responsible for the transposition. For the purposes of this study, the important point is that the transposition problem furnished a test of the amygdalectomized animal's reaction to two sets of normally related discriminative stimulus events.

The results do not, e.g., rule out the possibility of a more basic impairment in discrimination processes. If this is true, however, then the effect must be of a highly selective nature since amygdalectomy has not generally been found to impair visually guided test performance (Mishkin, 1954; Mishkin & Pribram, unpublished data; Pribram & Bagshaw, 1953). It may also be added that the lesions, as described elsewhere (Schwartzbaum, 1960), did not generally encroach upon isocortical sectors of the temporal lobe known to subserve visual functions (see Rosvold, 1959). But more direct comparisons between the effects of such lesions are nevertheless in order.

In any event, the results of the present study make one conclusion inescapable: amygdalectomy impairs functions that are involved in determining discriminative as well as reinforcing properties of stimuli. Whether these functions can be reduced to a common denominator in terms of generalization or transfer as suggested here can be established only when the limits of the findings are further explored.

Summary

A classical form of transposition problem was used to test the assumption that amygdalectomy impairs processes necessary for the generalization of a learned response from one set of stimuli to another.

Four monkeys with bilateral lesions of the amygdaloid complex and four normal monkeys were trained on a brightness discrimination with a dark gray and a medium gray (positive stimulus). They were then tested for transposition of response by pairing the medium gray with a light gray (both stimuli positive). Based on the transposition findings, a sequential discrimination was presented. The medium gray was paired randomly on different trials with either one of the other grays, but remained as the positive stimulus throughout. The following results were obtained:

1. Amygdalectomy did not appreciably affect the initial learning of the brightness discrimination.

2. The lesion did impair generalization of response to the transposition stimuli. In contrast with the normal pattern of transposed responses, three out of four amygdalectomized monkeys responded in what appeared to be a random manner.

3. Amygdalectomized monkeys were also inferior to the normal animals on the sequential discrimination, the differences again being associated with the presentations of the transposition stimuli.

The results lend support to the original hypothesis and indicate that amygdalectomy impairs functions that are involved in determining discriminative as well as reinforcing properties of stimuli.

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(Received August 14, 1959)