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RESPONSE TO CHANGES IN REINFORCING CONDITIONS OF BAR-PRESSING AFTER ABLATION OF THE AMYGDALOID COMPLEX IN MONKEYS¹

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Lesions in the region of the amygdaloid complex were found recently to affect the reinforcing values of different amounts of food reward (Schwartzbaum, in press). Amygdalectomized monkeys showed less change in barpressing activity than did normal animals when the amount of reinforcement was either increased or decreased. The present experiment explored this problem further. It was intended, first of all, to re-examine the changes in bar-pressing with an increase in reward. Somewhat different conditions from those used previously were adopted so that (a) confounding variables that relate to satiation could be eliminated, and (b) the time course of any lesion effects could be more accurately determined. The experiment was also designed to study the response of amygdalectomized animals to other forms of shifts in reinforcing conditions. For this purpose, an extinction and reconditioning procedure was employed.

The changes in reinforcing conditions were correlated with a stimulus that was presented for a brief period once during each test session of bar-pressing. The termination of the stimulus coincided with the delivery of a reward that differed from that otherwise available for bar-pressing. A measure of response to the shifted reinforcing conditions could be derived by comparing the number of bar-presses during the stimulus period with the number of bar-presses during the preceding control period.

METHOD

Subjects

Ss were eight rhesus monkeys that had been used previously in studies of operant behavior with different conditions of food deprivation and reinforcement (Schwartzbaum, in press). In four of the animals, the amygdaloid complex and a part of the anteromedial temporal cortex had been resected bilaterally. Reconstructions and cross sections of the lesions are contained in the report previously cited. The other four animals had received a sham operation which duplicated the lesion procedure except for the neural resection.

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A total of 8 to 13 months separated the start of the present experiment from the time of surgery.

Apparatus

A sound-insulated Skinner box was used, as described elsewhere (Schwartz-baum, in press). It contained a lever, measuring 4.0 cm. in length and 0.6 cm. in diameter, which required a minimal force of 170 gm. to open a contact on a switch. Reinforcements were delivered into a food cup situated beneath the lever. Two 25-w electric bulbs were mounted above the test cage in the box. One was frosted, the "house light," and the other was red.

Procedure

Preliminary.—The animals were retrained for six sessions to press the bar in accordance with a 2-min. "fixed-interval" contingency of reinforcement. At least 2 min. had to elapse after a reinforcement before the next one became available. The reward consisted of a 45-mg. Peanut Lab Chow pellet (P. J. Noyes and Co.) which the animals had experienced previously. Tests were administered once daily, six days a week. Each test lasted 30 min. The reward was always programmed to reinforce the first response in a session. Ss were maintained throughout the experiment on a daily diet of 8 to 10 Purina Lab Chow pellets and a quarter of an orange. They were fed about two hours after each session.

Conditioning.—A red light was substituted for the house light once during each test session. The stimulus appeared immediately after one of the reinforced responses, and continued for at least two minutes until the succeeding reinforced response. The reinforcement paired with the termination of the stimulus differed from that otherwise available for bar-pressing, i.e., the 45-mg. pellet. In order to minimize any temporal discrimination, the interval in which the stimulus appeared was varied randomly from session to session. However, the stimulus never appeared before the third or after the ninth 2-min. interval. This restriction made allowance for a pre-stimulus control period, and it insured that the stimulus presentation would not be omitted because of delays in bar-pressing. The random order of presentations was the same for all Ss.

In Sessions 1 to 6 of conditioning, the stimulus was paired with two ½-gm. Peanut Lab Chow pellets (P. J. Noyes and Co.). These pellets, with which Ss had also been tested previously, are 1.0 cm. in diameter and 0.5 cm. thick, and have the same composition as the smaller ones. This made it possible to study the conditioning of an increase in rate of bar-pressing to the stimulus as a function of its association with a substantially increased amount of reward.

In subsequent conditioning sessions, two whole peanuts whose combined weight averaged about two grams were substituted for the ½-gm. pellets. It was hoped that the preference for peanuts over pellets (unpublished data) together with the larger amount of the reward would increase the response to the

stimulus and thus provide a more sensitive test of lesion effects. The stimulus was paired with the peanuts for 11 consecutive sessions.

"Extinction".—The enhanced responding conditioned to the stimulus was subjected to "extinction" by omitting the food reward at the termination of the stimulus. Other visual and auditory stimuli associated previously with the delivery of the reward continued as before. This change in conditions applied only to the reward that was paired to the stimulus. Reinforcing conditions in the absence of the stimulus remained the same throughout the study. The extinction procedure was continued for 11 consecutive sessions.

The use of the term, "extinction," must be qualified because the termination of the stimulus was still contingent upon a bar-press. In order to reinstate the regular conditions of reinforcement, the animal had to respond. Consequently, complete cessation of bar-pressing in the presence of the stimulus would not be expected.

Reconditioning.—In the last phase of the experiment, bar-pressing was reconditioned to the stimulus by again pairing the stimulus with two whole peanuts. This procedure was continued for a total of 11 consecutive sessions.

Treatment of the data.—The magnitude of response conditioned to the stimulus was expressed in terms of a "rate index." This index relates the number of responses made during the 2-min. stimulus interval to the number of responses made during the immediately preceding 2-min. control interval according to the formula (A - B)/(A + B); A = responses during the stimulus interval, and B = responses during the control interval. A ratio form of expression seemed appropriate since arithmetic differences between stimulus and control rates tended to correlate positively with the control rates.

The rate index data were treated statistically by a method of trend analysis (Alexander, 1946) to check primarily for any group differences in the rate of change in performance. Although the limits of the rate index are set at \pm 1, a transformation of the scores was not required for the analyses since the scores never approached these extremes.

RESULTS

Bar-pressing activity of the two groups was not distinguishable on the test sessions which preceded the presentation of the stimulus. The normal monkeys averaged 154 responses per session (range of 118 to 205), compared with a mean of 199 responses per session (range of 124 to 267) for the amygdalectomized animals. Nor did the groups differ at any time in the number of bar-presses made during the 2-min. control intervals. These control values showed relatively little fluctuation during the sequence of changes in stimulus-reward conditions. Mean values for the different conditions ranged from 12.2 to 17.6 responses for the normal anmials, and from 14.1 to 17.8 responses for the amygdalectomized animals.

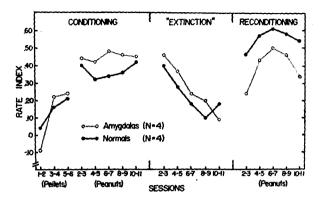


FIG. 1. Mean rate index of response to the stimulus as a function of its associated shift in reinforcing conditions. The rate index is defined as (A-B)/(A+B) where A= number of bar-presses during stimulus interval, and B= number of bar-presses during the preceding control interval.

Fig. 1 illustrates the changes in magnitude of response to the stimulus as a function of the stimulus-reward conditions. The data are plotted for successive pairs of sessions. Where a change in reward conditions occurred, the results from the initial session are excluded since the Ss could not discriminate the change until after the termination of the stimulus. Table 1 contains a summary of each of the trend analyses performed on the conditioning and extinction data.

TABLE 1
SUMMARY OF TREND ANALYSES OF RATE INDEX DATA FOR
CONDITIONING AND "EXTINCTION"

Source		ondition (Pellets)		Conditioning (Peanuts) II			"Extinction" III		
	df	MS	F	df	MS	F	df	MS	F
Over-all slope	1	.2601	24.08†	1	.0032		1	.4351	31.30†
Between group slopes	1	.0272	2.52	1	.0000		1	.0097	
Between individual slopes	6	.0394	3.65	6	.0180	1.62	6	.0417	3.00*
Over-all deviation from linearity	1	.0408	3.77	3	.0046		3	.0127	
Group deviations from linearity	1	.0170	1.57	3	.0051		3	.0093	
Individual deviations from estimation (error)	6	.0108		18	.0111		18	.0139	
Between group means	1	.0003		1	.0592		1	.0221	
Between individual means	6	.0681		6	.1465		6	.1059	

^{*}P < .05 †P < .001

It can be seen that amygdalectomy had no effect upon the performance for the larger or otherwise more preferred kind of reward. Both groups ex-

hibited a moderate increase in response for the larger amount of reward, and a more substantial increase for the peanuts. Indeed, the change in reinforcing conditions almost doubled the rate index. Of particular interest is the stability of this enhanced response for the peanuts. The trend analysis (Table 1, Part II) indicates no systematic changes in performance. The apparent group differences do not even approach statistical significance.

An orderly pattern of extinction occurred with the omission of the stimulus-paired reward. But again no reliable lesion effects are evident. Analysis of other measures of performance such as temporal patterning of responding and poststimulus responding also yielded negative results.

Reconditioning proved to be the only test condition that distinguished the two groups. Comparison of reconditioning with the conditioning reveals a difference with respect to the change in performance. These data are presented in Table 2. Conditioning is defined by the mean rate index for Sessions 2 to 11 with the peanut reward. Using these values as a base line, it can be seen that all of the normal Ss increased their response to the stimulus on reconditioning above the level set during conditioning. The brain-damaged Ss, on the other hand, showed no consistent change. The same is true if only the peak levels of reconditioning are considered (Sessions 4 to 9). With no overlap between the groups, these effects are significant at the .028 level by a two-tailed Mann-Whitney U test.

TABLE 2

MEAN RATE INDEX OF PERFORMANCE FOR EACH ANIMAL AND GROUP
DURING CONDITIONING AND RECONDITIONING

Test	Normal Ss					Amygdaloid Ss					
	1*	2	3	4	Mean	5	6	7	8	Mean	
Conditioning-peanuts Sessions 2-11	.37	.17	.60	.36	.37	.65	.36	.28	.51	.45	
Reconditioning Sessions 2-11	.44	.40	.75	.62	.55	.53	.43	.28	.35	.40	
Reconditioning Sessions 4-9	.49	.45	.78	.63	.59	.62	.46	.33	.46	.47	

^{*}Subject 1 was No. 439; 2, 443; 3, 441; 4, 447; 5, 397; 6, 405; 7, 438; 8, 442.

The over-all pattern of reconditioning, however, would appear to be the same for both groups. A fairly consistent decline in performance occurred during the last few sessions. Thus, in an analysis of the over-all trends by the method of orthogonal polynomials, the curvilinear quadratic component was highly significant (P < .001).

DISCUSSION

It is quite clear that, at least under certain conditions, amygdalectomized

monkeys can respond effectively to quantitative or qualitative shifts in food reinforcement. These results constrain the generality of previous findings of decreased responsiveness to changes in amount of reinforcement (Schwartzbaum, in press). The ability of the brain-damaged animals to adjust to such changes would seem to depend on other, as yet unspecified, variables. The same is true for extinction of responding after omission of the reinforcement. Negative results obtained in this and the preceding study are in sharp contrast to the slower extinction reported by Weiskrantz (1956).

On the basis of these findings, it would seem less likely that changes in the reinforcing properties of stimuli arise from direct involvement of the lesion in processes which are specific to reinforcement. If this were so, one might expect more pervasive effects on differential performance for different kinds or amounts of reward. The selectivity of the lesion effects is borne out by other unpublished data of Schwartzbaum and Wilson on food preferences for different amounts and kinds of foods, using paired-comparison techniques. It is further underscored by the present findings with respect to conditioning and reconditioning.

The effects of the lesion on reconditioning appeared to arise from a change in performance by the normal animals. Their response to the stimulus on reconditioning, in contrast to that of the amygdalectomized animals, exceeded the levels set during conditioning. In this respect, their performance was enhanced. It would appear that events associated with the interpolated extinction were responsible for this enhancement. (a) There was no reliably increasing trend of performance evident during conditioning, and (b) with the spacing of the stimulus presentations, it is unlikely that the enhancement represents a reminiscence phenomenon.

Such augmenting effects of extinction upon subsequently reinforced behavior have been reported before. Lauer and Carterette (1957) found that extinction of a running response in the rat increased starting speed during reacquisition of the habit. The increase in operant rate after "time outs" from positive reinforcement are introduced (Ferster, 1958) may also belong in this class of phenomena. Indeed, we may be dealing with a special case of non-reward "frustrative effects" (Amsel, 1958). The enhanced performance on reconditioning may, in this sense, derive from aversive properties that become conditioned during extinction to competing responses of bar-pressing or to the light stimulus itself. The quadratic form of the reconditioning function, also evident in the Lauer and Carterette data (1957), is perhaps in keeping with this possibility. However, the possibility cannot be ruled out that the enhancement represents a "contrast effect," as occurs with shifts in amount of reinforcement (e.g., Collier & Marx, 1959; Schrier, 1958). Thus, it may reflect an increase in the reinforcing value of the peanut reward. The rein-

forcing value of a reward may be contingent not only upon other reinforcing agents in the situation, but also upon the antecedent conditions associated with the reward itself.

The lesion impairment may, thus, relate (a) to an effect on the aversive control of behavior (Brady, Schreiner, Geller, & Kling, 1954; Weiskrantz, 1956), although this was not evident in the extinction performance and/or (b) to decreased responsiveness to shifts in amount of reinforcement (Schwartzbaum, in press) involving contrast effects.

SUMMARY

The experiment provides additional data on the response of amygdalectomized animals to shifts in reinforcing conditions of bar-pressing. The changes
in reinforcing conditions were paired with a stimulus that was presented during one of the intervals of a 2-min. "fixed-interval" schedule of reinforcement.
The termination of the stimulus coincided with the altered reinforcing conditions. Four normal and four amygdalectomized rhesus monkeys served as
Ss. Conditioning of an increase in rate of response to the stimulus when it
was paired with a substantially larger amount or otherwise more preferred kind
of reward was not impaired by the lesion. Similarly, extinction of the increased
rate was unaffected by the lesion. Group differences emerged on reconditioning.
Events associated with extinction appeared to be responsible in the normal
animals for an increased response to the stimulus on reconditioning above the
level set during conditioning. This augmenting effect of extinction upon
subsequently reinforced behavior was not found in the amygdalectomized animals.

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