RETENTION AND LEARNING
IN NORMAL AND BRAIN-LESIONED RHESUS MONKEYS
AFTER A SIX-YEAR INTERVAL

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ABSTRACT

RETENTION AND LEARNING IN NORMAL AND BRAIN-LESIONED RHESUS MONKEYS AFTER A SIX-YEAR INTERVAL

By

Bruce Ray Marshall

Four experiments were conducted to assess retention and new visual discrimination learning by four normal and three operated (posterior association area lesions) rhesus monkeys remaining from a previous study by Raisler (1966). In the previous study, one lesioned male showed performance comparable to the controls while the two lesioned females showed little evidence of postoperative retention or new learning.

In Experiment I, all subjects received training on five new three-dimensional pairs. Each pair was presented for a maximum of three days (40 trials per day). In addition, those subjects who did not reach criterion on two or more of the five pairs also received more extended training on additional pairs. The results indicated that all lesioned subjects could learn three-dimensional discrimination problems if given extended training on individual pairs. Performance on pairs presented for a maximum of three days of training, however, was comparable to performance on similar pairs in Raisler's (1966) study.

Experiment II involved a retention measure of

previously presented three-dimensional pairs. Each subject received two trials with each of 32 of a set of 64 pairs learned six years previously under four conditions of trial and problem sequences. Three of the four normal subjects showed significant retention scores (about 75%) while none of the lesioned subjects demonstrated any evidence of retention. The lack of retention by the lesioned male who had originally shown learning was attributed to a memory deficit. Some evidence was also found suggesting that conditions of trial and problem sequence during initial learning can affect retention.

In Experiment III, the effect of reversing part of the sequence of operations in the presentation of a trial was tested. The manipulation of raising the opaque door of the WGTA following the placement of the Klüver tray near the test cage (rather than the reverse sequence) resulted in increased errors for two lesioned subjects but no differences for the normal controls.

In Experiment IV, three planometric form and three planometric color problems were presented to determine the saliency of color and form cues to the lesioned subjects. The lesioned male who had demonstrated learning comparable to the normal controls met criterion on nearly all color problems and one form problem. The marked increase in errors for this subject, however, indicated that color cues alone were not sufficient to account for this subject's normal learning scores on three-

dimensional problems. Moreover, the other lesioned subjects showed no evidence of discrimination of either color or form.

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By

Bruce Ray Marshall

A THESIS

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To Grandpa (671)

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I first wish to thank the members of my committee. Dr. Lester M. Hyman's criticisms of my first proposal provided me with a better understanding of the assets and liabilities of various research designs. Dr. John I. Johnson's suggestions of the possibility of cueing led to what I consider to be the most interesting and as yet uninterpretable aspect of this study, that is, the factor responsible for the sudden learning in the latter part of Experiment I. In addition, Dr. Johnson's later suggestions concerning the organization of this thesis provided me with a more intuitive understanding of the purpose and format of a research report.

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INTRODUCTION

The functional significance of the posterior association area in the rhesus monkey has been a major research question over the past three decades. Since Klüver and Bucy's (1938) report of "visual agnosia" following bilateral temporal ablation, numerous investigators (for a review, see Mishkin, 1966, or Wilson, 1968) have dealt extensively with this issue. Unfortunately the results of their efforts have in general only magnified the complexity of the problem. To date, no parsimonious explanation exists for the detrimental effect of the posterior association area lesion on visual discrimination behavior nor has the controversy been completely resolved concerning the importance of various subareas of the posterior association area and their possible interconnections with striate areas.

Pribram (1954) has strongly implicated the inferotemporal area as prepotent for visual discrimination problems, particularly the two-dimensional patterns. The finding of a severe, but not permanent, pattern discrimination deficit following bilateral inferotemporal lesions has been consistently replicated both by Pribram (Pribram, Blehert, & Spinelli, 1966) and by others (Mishkin, 1966;

Wilson,Wilson, & Sunenshine, 1968). Pribram (1958) suggests that the inferotemporal cortex exerts efferent control over striate cortex via subcortical structures and also denies the possibility of any cortico-cortical connections from inferotemporal cortex to striate cortex via prestriate areas.

Mishkin (1966), on the other hand, argues against the possibility of efferent control via subcortical nuclei, and proposes that the prestriate areas exhibit a high degree of equipotentiality as a cortical relay between inferotemporal and striate areas. He suggests that removals or crosshatching of prestriate areas have been incomplete possibly due to the danger of intrusion into geniculostriate radiations. Mishkin further proposes that recovery of pattern discrimination following bilateral inferotemporal lesions is contingent upon intact prestriate areas, and has presented evidence (Ettlinger, Iwai, Mishkin, & Rosvold, 1968) that the combination of inferotemporal and complete prestriate lesions performed in either order results in a permanent pattern discrimination deficit. The finding of a permanent pattern discrimination deficit, however, is not new. Harlow and his colleagues (Warren & Harlow, 1952; Raisler & Harlow, 1965) have previously reported such an effect following posterior association lesions although their subjects did not receive such extensive ablations of inferotemporal cortex.

Returning to the question of the nature of the observed deficit, it was stated that no parsimonious explanation has been presented. That is not to say that simple explanations have not been proposed but rather that one-factor explanations of attention or sampling deficits (Butter, 1968; Stamm & Knight, 1963), retention deficits (Weiskrantz, 1964; Wilson et al., 1968), or inability to withhold responding (Schilder, Pasik, & Pasik, 1968), have not been sufficient to encompass all of the reported results. Any theory of cortical functioning in the rhesus must be able to account for the results of a number of intriguing studies. First, the effects of inferotemporal or posterior association lesions seem to be specific to certain aspects of the visual discrimination task. It is a well established fact that visual field defects or deficiencies in eye-hand coordination in picking up small objects, are not usually found following inferotemporal lesions (Weiskrantz & Cowey, 1963; Wilson & Mishkin, 1959). Yet these inferotemporal animals show gross deficiencies in discriminating pairs of objects or patterns in the formal testing situation.

Second, the behavioral effects of the inferotemporal lesion appear to be specific to the visual modality. Experiments using analogous training procedures in olfactory, tactile, and auditory modalities have not resulted in such large deficits following inferotemporal lesions (Brown, Rosvold, & Mishkin, 1963; Schilder et al., 1968; Weiskrantz & Mishkin, 1958).

Third, preoperative overtraining on a stimulus pair does not lead to the pronounced deficit following temporal ablation (Chow & Orbach, 1957; Orbach & Fantz, 1958). The effect of overtraining is specific to the overtrained pair, i.e., non-overtrained pairs result in the characteristic deficit in the same subjects.

Fourth, the degree of deficit and permanence of the deficit following inferotemporal or posterior association area lesions depends upon the type of discrimination problem. Warren and Harlow (1952) report, following posterior association lesions, almost complete recovery of the ability to discriminate three-dimensional object pairs (varying in color, form, and size). Although object discriminations were not impaired after a 14-month postoperative interval containing extensive discrimination training, no substantial evidence for learning was found for two-dimensional form or size discriminations. A later study by Raisler and Harlow (1965) suggests that recovery of three-dimensional discriminations may depend upon utilization of color cues. This finding is consistent with the above chance performance on color discriminations in Warren and Harlow's data as well as Warren's (1953) results showing the saliency of color cues in the intact rhesus.

Although it is clear that extended postoperative training can lead to high levels of performance on certain visual tasks, the question of whether this recovery can be spontaneous remains unanswered. Harlow (1939) found no evidence of spontaneous recovery in monkeys on patterned strings problems following unilateral occipital lobectomies. He interpreted the results of retraining as learning to counteract the effects of a hemianopsia. Chow (1952) found only minimal evidence of recovery without retraining. Of two monkeys that had been in darkness for three months postoperatively, one monkey showed improved post-darkness retention scores (in comparison with postoperative retention scores) on both preoperatively learned color and brightness discriminations. In addition two other monkeys had received three months of postoperative training on new discriminations (rather than darkness). They showed even greater (and more consistent) retention of the three preoperatively learned discriminations following the additional training. Moreover, other studies have led to somewhat contradictory results. Stewart and Ades (1951) have presented evidence of retention of an auditory discrimination in a shock avoidance task where the superior temporal gyri were removed in two successive operations separated by seven days or longer. Shorter interoperative intervals did not result in such high levels of retention. In a later study Meyer (1958) has attempted to clarify Stewart and Ades' finding. Meyer's results indicate that with an interoperative interval of 12 days, a brightness discrimination was retained in rats who spent the interoperative interval in their home cages but was not retained in rats who spent the interval in darkness. As Meyer has stated, his results demonstrate the importance of postoperative experience and suggest that relearning may not have to be specific to the formal test situation.

The aforementioned studies of spontaneous reorganization have in general dealt with animals lesioned during their adult life. The effects of lesions performed early in life suggest a rather different picture. Experiments on monkeys with lesions of frontal association cortex (Harlow, Akert, & Schiltz, 1964), motor cortex (Kennard, 1942), and posterior association cortex (Raisler & Harlow, 1965), all show less severe deficits from early lesions than from lesions performed on the adult monkey. Such findings are analogous to the recoveries from aphasia in human patients following cerebral trauma at an early age (Penfield & Roberts, 1959).

A later study by Raisler (1966), however, has resulted in contradictory evidence regarding the effects of early versus late lesions. This study, which dealt with posterior association area lesions including major portions of inferotemporal cortex, did not result in the expected decreased deficits in the early lesion group. Although the histological processing has been partially completed for the early lesion group, the older lesioned subjects as well as the older controls have not yet been sacrificed.

The present study is a followup assessment of the visual discrimination capabilities of the remaining subjects. The assessment approach, involving a series of short tests (e.g., Milner, Corkin, & Teuber's (1968) periodic testing of H.M., a patient with a severe hippocampal amnesia syndrome), was chosen to provide the most information concerning both retention over a six year interval and the nature and severity of the visual discrimination deficiencies of the remaining lesioned subjects. More specifically, this study attempted to answer four questions: (a) Can the lesioned animals which have demonstrated little evidence of postoperative learning meet criterion if given extended training on a single problem pair? (b) After a six-year interval, is there any evidence of retention of previously learned object discriminations and is this retention related to the lesion? (c) Can the sequence of operations in the presentation of a trial affect performance? and finally (d) Is the magnitude of the deficit in the lesioned animals related to the type of differences between the positive and negative stimulus (i.e. color versus form)?

METHODS

Subjects

The seven rhesus monkeys (*Macaca mulatta*) tested in all stages of this study served in a previous experiment by Raisler (1966). Four subjects (two males, two females) constituted the unoperated adolescent controls (Group 38N) of that study. The remaining subjects (one male, two females) were part of the adolescent operated group (38T) that received extensive bilateral posterior association area lesions, probably including major portions of inferotemporal cortex. Although histological confirmation of the extent of the lesions has not yet been accomplished, there is some suspicion that Monkey 672 may have a partial visual field deficiency due to an unplanned intrusion into the geniculostriate radiations.

Preoperatively all subjects received training using 16 three-dimensional (stereometric) and 16 two-dimensional (planometric) object pairs. Postoperatively testing included new three-dimensional pair learning, and retention and relearning of the two- and three-dimensional pairs learned preoperatively. In addition, all subjects postoperatively received two months of training on 64 pairs of objects under four different conditions of trial and problem sequences.

The results of the extensive postoperative testing indicated that two of the surviving subjects from the adolescent operated group showed essentially no evidence of retention or new object pair learning while the third subject showed abilities approaching, but not equalling, the unoperated controls.

Apparatus

Testing in all stages was accomplished using a modified Wisconsin General Test Apparatus (Harlow, 1949) attached directly to the front of the test cage. The test cage was located in a semi-soundproof room and was illuminated during testing by a light from the WGTA itself. The test cage consisted of a frame of wood to which the sides, floor, and roof of woven stainless steel cable were attached. The inside dimensions of the cage were 48"w. x 30"h. x 24"d., thus allowing considerable movement of even the largest male. The WGTA consisted of a box-like structure, open at two ends, suspended from the front of the test cage. The experimenter sat at one open end and looked through the box to the other open end at the front of the test cage. Between trials a vertical sliding door near the front of the cage could be lowered to occlude the subject's vision. During a trial, a Klüver tray (described in Raisler & Harlow, 1965) was pushed along the floor of the box to the front of the test cage. A piece of white cloth, suspended from the experimenter's end of the WGTA allowed viewing of the subject during a trial but prevented eye-to-eye contact. Ample lighting was provided by a flush mounting ceiling light attached to the inside roof of the WGTA.

Adaptation Procedure

Adaptation prior to testing consisted of two stages. First each subject was placed in the test cage for a minimum of 15 minutes per day for a total of eight days. When necessary, additional training was given to those subjects who entered the transport cage reluctantly. When each subject had displaced a wooden block to obtain a food reward with latencies consistently under five seconds in 10 daily trials on two consecutive days, then all subjects received an additional 10 trials on the day immediately preceding the onset of testing.

EXPERIMENT I: NEW LEARNING

The first stage of testing provided a rough estimate of new object pair learning.

Method

A total of 9 stimulus pairs were randomly selected from a population of 75 new stereometric pairs consisting of multicolored, multisized, and multishaped junk objects mounted on white 3" x 3" masonite bases. These new pairs had been randomly paired subject to the restriction that the members of a pair differ in one color.

All subjects received training with five new three-dimensional pairs at the rate of one pair per day, 40 trials per day, until the criterion of 32 correct of 40 trials on a single day had been met or until three consecutive days of training on that pair had failed to produce criterial performance. If at the end of the fifth problem, a subject had not reached criterion on two or more of the five problem pairs, at least one additional pair was given until criterial performance was met or until at least 12 days of testing had failed to produce criterial performance.

In the first part of Experiment I (testing on five pairs for a maximum of 120 trials each) as well as in part of the extended training given to individual subjects, a trial was defined in the usual manner. That is, the Klüver tray with the positive stimulus covering the baited foodwell and the negative stimulus covering the empty foodwell was pushed to the front of the test cage after or during the time the door was raised. Following a displacement of either stimulus by the subject, the tray was immediately pulled back and the door lowered. During the intertrial interval, the previous response was recorded and the preparation for the next trial was accomplished (baiting and positioning of the positive and negative stimuli). Positioning of the positive stimulus was varied according to a Gellermann (1933) series. During the latter part of the extended training, however, certain procedural variations in the presentation of a trial were achieved. These variations included pushing the tray to the front of the cage prior to raising the door, the inclusion of an occasional correction trial, and deliberate attempts to mask any auditory cues that occurred in the baiting process. These variations were presented primarily as a check for cueing.

Results

Number of problems learned and total errors for the first five new stereometric pairs are presented in

Table 1. None of the normal subjects had any difficulty in making any of the discriminations whereas the lesioned subjects showed highly variable performance. The lesioned male (671) showed performance comparable to the controls while the two lesioned females showed either chance performance throughout (672) or above chance but below criterial performance (670) on the third training day of four of the five problems.

Since subjects 670 and 672 did not reach criterion on two or more of the first five problems, they received training on three and four additional pairs, respectively. For the first 10 days of testing on the first additional problem, Monkey 672 remained at chance. On days 11 and 12, however, above chance but below criterial performance began to appear. As a result an additional day of training was given. On this day conditions of presentation were varied partially to eliminate the possibility of cueing the subject through unintended means. Surprisingly enough, on day 13 Monkey 672 made only 2 errors in 36 trials. One additional problem given with the varied presentation conditions was learned within two days. The third new problem for Monkey 672 was given with the standard method of presentation, and again criterion was met, but only after six days of training.

Monkey 670 met criterion in four days each on two additional pairs with the standard method of presentation.

Table 1

Number of Problems Learned to Criterion and Total Number of Errors (Experiment I)

Group	Subject	Problems Learned	Total Errors
Normal	666	5	12
	667	5	16
	668	5	26
	669	5	6
Temporal	670	1	221
	671	5	10
	672	0	304

This subject also received two pairs with the varied presentation conditions. Criterion on these last two pairs was met within two and three days respectively.

Summarizing the results of the additional testing, it appears that given sufficient training on individual pairs, both subjects 670 and 672 can learn new stereometric problems, although their performance on the first three days may not suggest any signs of improvement. The possibility that method of presentation of a trial can affect performance was suggested and provided the basis for Experiment III testing.

EXPERIMENT II: RETENTION AFTER SIX YEARS

The second experiment provided a retention measure of stereometric pairs that had been postoperatively learned six years previously. The first trial with each pair was considered as the pure retention measure, whereas a second trial performance was included to provide a crude measure of the learning set performance if, and only if, no retention was demonstrated. This stage of testing was of interest primarily because of the unusually long interval since the original learning.

Method

Stimuli consisted of a sample of 32 of the 64 stereometric problem pairs (the first four pairs of each of the eight sets of eight pairs) from Experiment II of the previous study (Raisler, 1966). In that study all subjects received training on 64 stereometric problem pairs under four conditions of trial and problem sequences. A problem was defined as the presentation of a stimulus pair, i.e., a positive and a negative stimulus. During two months of testing, each subject twice received one week of training on each of the four conditions, subject to the restriction that both the first and the second months

of training each include all of the four conditions. During each week of testing (during any condition), each subject received five days of training on 8 new problems. On any day of testing, for all conditions, each subject received 8 problems per day, 5 trials per problem, for a total of 40 trials per day. What varied in the four conditions was the sequence of the 40 daily trials with the 8 problems. In condition "1", each subject received 5 trials with problem 1, then 5 trials with problem 2, then 5 trials with problem 3, etc., until 8 problems had been presented for a total of 40 trials per day. For the remaining four days of that condition, the same 8 problems were presented in the same sequence of trials. In condition "2", each subject received trial 1 with each of the first 2 problems, followed by trial 2 of each of the first 2 problems, etc., until each of the 2 problems had been presented for 5 trials. This sequence was followed by three more pairs of problems presented in the same sequence for a total of 8 problems and 40 trials. The remaining four days of condition "2" training each contained the same sequence of 40 trials with the same 8 problems. In condition "4", each subject received trial 1 with each of the first 4 problems, followed by trial 2 of each of the first 4 problems, etc., until each of the first 4 problems had been presented for 5 trials. Four more problems were presented in the same manner for a

total of 40 trials and 8 problems. As in the other conditions, the remaining four days of training contained the same sequence. In condition "8", the sequence of trials was presented in an analogous fashion, i.e., trial 1 of each of the 8 problems, followed by trial 2 of each of the 8 problems, etc.

In the present study, during eight testing days, each subject received a sample of 32 of the 64 pairs from the four conditions varying in problem and trial sequences. Four problems, two trials per problem, were presented on each of eight days. To maximize retention the 32 problems were presented in the same order as each subject initially experienced them. The same method of presentation of a trial (i.e. without correction, etc.) was used as in the first part of Experiment I.

Results

The retention scores on trial one for both the lesioned and control subjects are presented in Table 2. Summing across conditions for each subject, it is evident that three of the normals had total correct scores greater than or equal to 23 ($H_o: N \leqslant 16$, $p < .01$, one-tailed test, binomial distribution). Although the use of the binomial does allow treatment of the individual subject, the overall α level for the combined set of tests of significance will be contingent upon the number of tests. The most reasonable *a priori* number of

Table 2

Six-Year Retention Scores of Pairs Presented Under Four Conditions of Trial and Problem Sequences

Group	Subject	Condition				Total Correct	
		1	2	4	8		
Normal	666	7	5	5	7	24*	(13)
	667	4	6	7	7	24*	(19)
	668	4	1	3	8	16	(21)
	669	5	5	5	8	23*	(12)
	Mean	5.00	4.25	5.00	7.50	21.75	(16.25)
Temporal	670	6	2	4	5	17	(16)
	671	5	4	4	3	16	(18)
	672	2	6	3	2	13	(16)
	Mean	4.33	4.00	3.67	2.50	15.33	(16.67)

* Indicates significant retention score ($p < .05$, binomial distribution).

( ) Indicates total correct trial one performance scores from Raisler's (1966) study.

tests is five, since only five animals can be expected to retain, the five who originally learned. Given five possible tests, to maintain an overall α at .05 then requires that each significance test be made at the .01 level. It can easily be shown that when p is very small, the probability of the union of a set of equal p's will be almost identical to their sum. In addition, the test of the null hypothesis $\mu \leqslant 16$ yields virtually the same value for α ($t = 2.98$, $df = 3$, $p < .05$).

For comparison, the first trial performance scores for the same 32 pairs in Raisler's (1966) study are presented in parentheses in Table 2. The mean of 16.25 for the four normal monkeys obviously is not significantly different from the expected value of 16. The only subject (668) whose first trial scores six years ago approached significance is also the subject who demonstrated no evidence of retention. It appears reasonable to assume that the variability of the scores for the original trial one scores reflects only a random process. Granting this assumption, the test of a retention score against the null hypothesis, $N \leqslant 16$, is a valid approach.

A separate treatments by subject analysis of variance was applied to each group for the first trial retention scores and also for the second trial relearning scores (Table 3). Only the analysis of the normal group's trial one scores was significant ($F = 3.9$, $p < .05$).

Table 3

Trial Two Relearning Scores

Group	Subject	Condition 1	 2	 4	 8	Total Correct
	666	6	7	7	8	28
Normal	667	6	5	7	8	26
	668	8	6	5	6	25
	669	7	6	8	8	29
	Mean	6.75	6.00	6.75	7.50	27.00
	670	3	5	4	4	16
Temporal	671	6	5	5	4	20
	672	2	3	4	4	13
	Mean	3.66	4.33	4.33	4.00	16.33

Comparisons using the Newman-Keuls method indicated that the mean of condition "8" was significantly ($p < .05$) greater than the mean of condition "2".

Summarizing the results, it appears that three of the four normal monkeys and none of the lesioned subjects show evidence of retention of problem pairs presented six years previously. In addition, some minor evidence suggests that the trial and problem sequences during learning can affect the amount of retention.

EXPERIMENT III: PRESENTATION METHOD

The results during the extended training with subjects 670 and 672 (Experiment I) suggested that variations in the presentation of a trial might enhance performance. One of the symptoms in the Klüver-Bucy syndrome is the tendency to contact stimuli immediately. Such a tendency might result in chance performance due to the inability to withhold responding to the incorrect stimulus, thus blanketing any ability to make the visual discrimination. Generally, the presentation of a trial involves raising the opaque door and pushing the Klüver tray to the front of the cage. It was reasoned that after extensive training preoperatively, the stimuli associated with the approaching tray might become effective initiators of a complex sequence of behaviors which culminated in a response to one of the objects. Such an automatic sequence, although very useful to the intact animal, might interfere with performance in the lesioned animal if it could not withhold responding long enough to make the visual discrimination. If such a deficiency exists in these temporal animals, then any change in the procedure of the presentation of a trial could be expected to decrease the tendency to respond automatically, which might enhance performance.

Method

The subjects tested in Experiment III consisted of two lesioned monkeys (670 and 672) and two normals (666 and 669). Ten pairs of stimuli were randomly selected from the remaining members of the population of 75 new pairs described in Experiment I.

Each subject received five new stereometric pairs under each of two conditions. In the standard condition, as in most of Experiments I and II, each trial began with the raising of the door followed by the movement of the Klüver tray to the front of the cage. In the experimental presentation condition, the baited tray was first pushed up close to the door. Following the removal of the experimenter's hand, the door was raised. For both conditions each pair was presented for 40 trials during a single day using the non-correction method. The order of presentation of the five pairs for each condition was randomized within blocks of two for each subject.

Results

Individual error scores for each of the 10 pairs are presented in Table 4. Inspection of the data suggests that variation in the presentation procedure had little effect on the performance of the normal subjects whereas with the lesioned subjects, contrary to expectation, performance was slightly superior under the standard

Table 4

Number of Errors on Pairs

with Two Methods of Presentation

Group	Subject	Standard Condition (Pairs)						Experimental Condition (Pairs)					
		1	2	3	4	5	Σ	1	2	3	4	5	Σ
Normal	666	1	1	3	2	1	8	1	1	0	3	0	5
	669	1	1	3	0	1	6	2	1	0	2	0	5
Temporal	670	9	10	11	19	9	58	17	21	10	8	25	81
	672	8	14	20	15	25	82	17	10	31	21	22	101

method of presentation. Application of a three factor analysis of variance (mixed design, repeated measures on two factors) yielded virtually the same conclusion (*F* groups = 45.8, $p < .025$; *F* condition = 72.2, $p < .025$; *F* groups x condition = 105.8, $p < .01$). These α levels should be considered only as approximations since the other computed *F* ratios were all less than one. Such an outcome may indicate violation of the assumptions underlying the test, thus resulting in an increased probability of Type I error.

EXPERIMENT IV: COLOR OR FORM CUES

The purpose of Experiment IV testing was to compare discrimination performance on planometric pairs varying either in color or form. Of primary interest was the performance of Monkey 671 whose error scores were indistinguishable from the unoperated controls on new stereometric pair learning (Experiment I). On the basis of Raisler and Harlow's (1965) data showing the saliency of color cues in monkeys with posterior association area lesions, this subject was expected to show better performance on planometric color than planometric form problems.

Method

Stimuli consisted of six pairs (three color, three form) selected from the population of 200 planometric pairs described in Raisler and Harlow (1965).

The six pairs were presented to all subjects at the rate of one pair per day, 40 trials per pair. Training on each pair continued for a maximum of four consecutive days or until a criterion of 32 correct in 40 trials was attained on a single day. All subjects received the same sequence of color pairs alternating with form pairs.

Results

Total errors for color and form problems are presented in Table 5. All of the normal subjects met criterion on all six problems whereas the temporal subjects showed highly variable performance. Monkey 671 met criterion on two color problems (missed criterion on third problem by one error) and one form problem. The other lesioned subjects failed to reach criterion on any of the color or form problems. Although there are insufficient data from Monkey 671 to allow any meaningful statistical test, these results suggest that color is probably a more salient cue than form for this particular animal. These results do not, however, suggest that discrimination of color alone is sufficient to account for this subject's outstanding performance on object discriminations.

The data of each group were analyzed separately using a two-factor analysis of variance with replications (Hayes, 1965, pp.444-446). The results of both analyses failed to differentiate between color and form problems. In the analysis of the temporal group, the $\underline{F}$ for subjects was significant ($\underline{F} = 7.71$, $\underline{p} < .01$) although this finding leads to a trivial conclusion.

Table 5

Total Errors on Planometric Color and Form Problems

Group	Subject	Color Pairs				Form Pairs			
		1	2	3	Σ	1	2	3	Σ
Normal	666	17	7	2	26	8	56	3	67
	667	7	41	6	54	31	41	3	75
	668	23	24	5	52	17	52	60	129
	669	18	19	0	37	7	29	5	41
Temporal	670	74*	78*	66*	218	81*	78*	76*	235
	671	59	51*	5	115	63*	75*	34	172
	672	72*	87*	84*	243	79*	76*	81*	236

* Indicates non-criterial performance by the fourth day of testing.

DISCUSSION

Learning

The major finding of this study is that all the lesioned animals can learn object pair discriminations if given extended training on individual pairs. In all cases of extended training during the latter part of Experiment I, criterion was met in less than 600 trials. This criterial performance suggests that even the two lesioned females (670 and 672) might show performance comparable to the controls if given extended training on a number of new pairs.

Even though it is clear that the two lesioned females can learn, it is also clear that their deficits are still severe. The total errors for subjects 670 and 672 on the first five problems of Experiment I were 221 and 304, respectively. These error scores (as well as the error score of 10 for Monkey 671) are comparable to the postoperative scores on similar problems in Raisler's (1966) study. On the basis of pairs each presented for a maximum of three days (40 trials per day), there appears to have been little change in performance levels over the six year interval. Unfortunately Raisler's (1966) data provide no information about performance on pairs with more extended training. In no case in his study did training on a single pair exceed 120 trials. Therefore no absolute conclusion can be made as to whether any recovery (in the absence of retraining) has occurred over the six year interval. On the basis of the similarity of the error scores in the present study to error scores on comparable problems in Raisler's study, however, it appears unlikely that there have been substantial changes in the visual discrimination capabilities of these lesioned animals. A reasonable speculation would be that these lesioned animals could have demonstrated more evidence of learning in Raisler's (1966) data had they received more extensive training on individual pairs.

Retention

The results of Experiment II provide evidence of retention of object pair discriminations over the six year interval. On the basis of even such an insensitive measurement as trial one retention scores, three of the four normals showed above chance performance (75% correct). Considering the substantial improvement on the second trial scores for Monkey 668, one might also argue that her chance performance on trial one does not reflect an accurate assessment of her retention of the previously learned discriminations. In other words, the change in performance from trial one to trial two may be too large to be attributed solely to learning.

Some evidence was also found suggesting that the structuring of the sequence of learning trials may affect long-term retention. Pairs learned under condition "8" resulted in superior retention (borderline significance) when compared to pairs learned under condition "2". Had the amount of retention been more linearly related to condition, then a simple explanation could have been offerred. Under learning conditions that maximize interference (condition "8"), a subject could be required to utilize more features of each stimulus. A simple model based on additivity of cues could then be invoked to explain the increased retention. Under such maximized interference conditions, however, one might also expect slower learning of object discriminations. This result was not found in Raisler's (1966) study.

Of considerable importance is the failure to find a significant retention score for the lesioned male (671) whose postoperative object discrimination performance was comparable to a dull normal. Obviously no unassailable conclusion can be made regarding this subject's retention score since one normal also showed chance performance. It does seem plausible, however, to assume tentatively that a memory deficit is part of the temporal lobe syndrome, a conclusion made by Weiskrantz (1964) based on more extensive data. In addition, some purely observational evidence lends support to this conclusion. Monkey 671 periodically had to be shaped to enter the transport cage from either the home cage or the test cage. This shaping was rarely required if the subject had been tested the preceding day. If the inter-testing interval was greater than or equal to two days, however, reshaping was almost invariably required. Moreover, once in the testing situation, this subject was always cooperative, i.e., never refused to respond.

Presentation Method

The results of Experiment III suggest that minor variations in the sequence of operations in the presentation of a trial can affect the performance of the lesioned subjects. Contrary to expectation, the lesioned females made more errors when the door was raised after the Klüver tray was pushed to the front of the cage. Unfortunately, no satisfactory explanation can be provided for this outcome.

Color-Form

Experiment IV was of interest primarily due to the performance of the lesioned male (671) whose error scores were indistinguishable from the unoperated subjects. Consistent with the data of Raisler and Harlow (1965) showing the saliency of color cues in monkeys with posterior association area lesions, Monkey 671 met criterion on nearly all of the three color problems but met criterion on only one form problem. But considering the monkey's outstanding performance on three-dimensional pairs in Experiment I (an average of two errors per problem), the criterial performance on one form pair, and the marked increase in errors on planometric color discriminations, it cannot be concluded that the outstanding performance on stereometric pairs is due exclusively to the utilization of color cues.

Another interesting result is that neither of the lesioned females showed any evidence of learning planometric color or form problems. Considering the criterial performance on the stereometric pairs during the extended training on Experiment I, the lack of any indication of learning on the limited cue problems suggests that no single cue including color can account for the multicue learning of these lesioned females.

Individual Differences

The most perplexing problem suggested by these results deals with the subject of individual differences. Stated in a different way, the question is: How does one account for the huge variability in performance of these lesioned subjects? Suppose that one makes the assumption that all of the lesioned subjects could be performing as well as normals on object pair discriminations if given sufficient training. Such an assumption might be justified with the two females if histological evidence showed encroachment into unintended areas (there is suspicion of a partial hemianopsia in Monkey 672). One might then account for this recovery of object pair discriminations as due to the use of color cues as concluded by Raisler and Harlow (1965). Evidence for the saliency of color cues in the lesioned male (671) is presented in Experiment IV. This subject met or nearly met criterion on all three color problems but met criterion on only one form problem.

But given the assumption of recovery of object pair and color discriminations following combined bilateral inferotemporal, middle temporal, superior temporal, and prestriate lesions, as well as the earlier data of Raisler and Harlow (1965) indicating recovery following similiar lesions with less complete damage to inferotemporal areas, one would have to conclude that the additional lesion of inferotemporal cortex has not been shown to permanently affect object and color discriminations. Whether the additional inferotemporal lesion has a more devastating effect on pattern discrimination appears likely, since Ettlinger et al. (1968) have presented evidence for pattern deficits (2500 trials without criterial performance) following combined prestriate and inferotemporal lesions performed in either order. However, even the conclusion of permanent pattern deficits following combined prestriate and inferotemporal lesions does not explain the pattern discrimination performance of Monkey 671. This subject met criterion on one of the three two-dimensional form problems. Considering this subject's performance on the three-dimensional problems and the poorer (but still criterial) performance on the two-dimensional color problems, one could not conclude that the relearning of the object discriminations was solely due to the utilization of color cues. Moreover, the intended, but not yet confirmed, lesion in this subject presumably includes most of the neocortex removed by Ettlinger et al. (1968) as well as considerable destruction of middle and superior temporal gyri.

Now suppose that one has the complementary hypothesis that the performance of the two lesioned females are more representative of the population of monkeys with massive posterior association lesions (including inferotemporal cortex). One might argue that the lesioned male (whose performance is normal on object discrimination) has an incomplete lesion. On the basis of the two poorly performing females as representative of the hypothetical population it would have to be inferred that object and color discriminations are severely if not permanently disturbed by such extensive lesions. Unfortunately, no other relevant data are available. Either the lesions have not included such extensive inferotemporal damage (Warren & Harlow, 1952; Raisler & Harlow, 1965) or the subjects were not tested on object pair or color discriminations (Ettlinger et al., 1968). Moreover, even the speculation that massive cortical lesions lead to severe and permanent object and color discrimination deficits is not very appealing. DeValois, Smith, and Kitai (1959) have found lateral geniculate cells responsive to narrow wavelength bands, thus indicating that the neural basis for color discrimination at least exists subcortically.

Both of the previous speculative explanations for large individual differences in the lesioned group have been based on proposed differences in location and size of lesion. It has been implicitly assumed that the variance seen postoperatively reflects only variation in the surgical manipulation superimposed upon a standard preparation. In other words, the preoperative variation was assumed to be purely a function of random error.

Now suppose that one examines an additional hypothesis. More specifically, suppose that each subject comes to the test situation with his own particular method of visually sampling the environment. This peculiar method then interacts with the test situation, the experimenter, the stimuli, etc., resulting in a highly individualistic way of solving a problem like the visual discrimination task. Although different subjects may have different methods of solving the same problem, these different methods might be equally effective strategies for solving a simple problem like an object discrimination. Thus the preoperative variation would be small. Now superimposing a constant lesion onto a varying set of subjects might accentuate the differences postoperatively if the sampling methods of some subjects were more affected by the lesion than the methods of others.

It was a similar line of reasoning that led to varying of the presentation procedure in Experiment III. Although the results of Experiment III unfortunately do not lead to an understanding of the criterial performance exhibited by the two lesioned females during the extended training of Experiment I, other overt behaviors do provide a possible clue. During Experiment I, it was observed that the behavior of the lesioned male differed considerably from the behavior of the two lesioned females as well as the normal controls. This male had the habit of looking back and forth at the two stimuli a number of times (vicarious trial and error, VTE) prior to making a response on each and every trial. None of the other subjects consistently (if at all) showed such overt VTE's. One lesioned female (672) never showed such comparison behavior; this monkey rather consistently responded to the object closest to her.

Although the preceding discussion of some of the possible sources of variance in the lesioned group does not aid in interpreting the present results, it does demonstrate that not all explanations of differences need involve the notions of size and extent of lesions. It would be foolish to argue that variations in lesions are never related to variations in performance. The nature of the differences of the size and extent of the lesions often determine the nature of the differences in performance. Even with the present results, a lesion explanation may be the most parsimonious one. But it would also be foolish to argue that the postoperative performance differences always reflect lesion differences. In many cases, the performance differences are uncorrelated with the size and extent of the lesion. In these latter cases the most frequent approach has been to ignore the differences. If this variability does reflect something other than error, then systematic attempts should be made to study these differences. Any discipline that is forced to use small groups or even individual subjects cannot afford to overlook the source of these postoperative differences.

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