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VISUAL DISCRIMINATION WITH A SINGLE MANIPULANDUM FOLLOWING TEMPORAL ABLATIONS IN THE MONKEY

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The aim of this investigation was to determine what effect variation in the conditions of cue presentation and response availability has on the visual discrimination performance of monkeys with bilateral inferior temporal ablations. Six animals were trained on one of two versions of a test of successive brightness discrimination. Common to both versions of this test was the availability of a single lever, manipulation of which in the presence of the positive cue constituted the correct response. Performance on this test was compared with performance on a pattern discrimination, for which the customary simultaneous two-choice procedure was used. It was found that the temporal removals were followed by definite impairment on the pattern discrimination (as expected), but no consistent change in efficiency at brightness discrimination could be attributed to the lesions. Alternative interpretations, making reference to the amount of pre-operative training on the brightness discrimination or the lack of differentiation between the correct and alternative responses in this test, are discussed.

Introduction

Monkeys with bilateral inferior temporal lesions are, as a rule, impaired when required to select consistently between two formal response alternatives on the basis of two dissimilar and concurrent visual cues. It is established that the impairment in visual discrimination is not critically dependent upon the dimension along which the cues differ (e.g. size, brightness, hue or pattern), providing that the problem is of appropriate "difficulty" (Mishkin and Pribram, 1954; Mishkin and Hall, 1955). This parameter is defined by reference to the performance scores of unoperated animals on a given series of discrimination tests.

The conditions of cue presentation and response availability necessary for the manifestation of this discrimination deficit have not, however, been investigated as systematically as have the cue dimensions. An important exception to the predominant application of the classical "simultaneous" two-choice procedure (i.e. two cues with formal response alternatives are presented to the animal at one time) is the study of Pribram and Mishkin (1955). In their experiments only one of the two cues was presented on any given trial. The animal was required to make a given response in the presence of the positive cue and to avoid repeating this response when the negative cue was exposed. Under these conditions ("successive" discrimination) the post-operative deficit was at least as severe as with the simultaneous presentation of the same cues.

New conditions of cue presentation and response availability were devised for the present study. Using a Skinner-type automatic apparatus with a single manipulandum it was found possible to train monkeys to respond to changes in the overall luminance of an encompassing homogeneous field. The difficulty of this test could be graded by accurately varying the difference between the successive levels of luminance. Performance dependent on changes in overall luminance was contrasted with that

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dependent on an incremental light source superimposed upon a constant ground and with that on a standard simultaneous pattern discrimination. The aim of the investigation was to gain a wider understanding of the deficit which follows bilateral temporal ablations in monkeys by extending the range of test conditions.

METHODS

Subjects

Six immature and experimentally naive rhesus monkeys were divided at random into two groups. Animals T_1–T_4 were subjects in Experiment 1, animals T_5–T_6 in Experiment 2. Animal T_2 died following surgery. The animals weighed between 5 lb. 5 oz. and 6 lb. 12 oz. when testing began.

Operations and histology

All animals were given one-stage bilateral inferior temporal lesions on completion of their pre-operative training. The surgical and histological procedures have been described elsewhere (Ettlinger and Wegener, 1958). Reconstructions of the lesions and representative cross sections for animals T_1 and T_5 are shown in Figure 1. The lesions in the remaining animals are essentially similar. Broadly speaking, the average extent of removal is probably smaller than in the study of Pribram and Mishkin (1955), more particularly in the posterior direction.

Apparatus

For the tests of brightness discrimination, a globe of flashed opal diffusing glass (17½ in. diameter) was mounted centrally in a large refrigerator painted white, so that the globe's opening (9 in. diameter) faced downwards. A cage could be placed under the globe and was fitted with a movable false floor. When the top of the cage was pulled back a monkey could be hoisted into the interior of the globe. A lever and food chute projected for 2 in. into the opening of the globe on the level of the false floor when at its highest position. At a height of 8½ in. above the top of the globe a neutral density grating filter (20 in. by 20 in.) was installed. This could be silently varied by means of a cable mechanism and electrical motor housed in an adjoining room. Three G.E.C. circline fluorescent lamps (8¼ in. diameter, standard cool white; 12 and 16 in. diameters, standard warm white) were mounted concentrically against a reflector at 9½ in. above the filter, and supplied from a constant voltage source. A lens system, using the 16 in. tube as light source, allowed a disc of light ($\frac{9}{32}$ in. diameter) to be projected through the globe at 10½ in. above the lever. A shutter, operated silently by cables from the adjoining room, controlled the exposure of this incremental light spot. Its luminance could be adjusted independently of that of the globe, the former by means of filters in the optical system, the latter by the large grating filter. A loud buzzer served to mask all extraneous sounds.

For the simultaneous pattern discrimination a modified Wisconsin General Testing Apparatus was used.

EXPERIMENT 1

Training procedure (*see Table I*).

Pre-operative criterion training. Animals T_1–T_4 were first trained, in progressive stages, to criterion on a successive brightness discrimination where two levels in the overall luminance of the globe served as cues. Each week the four animals were given 5–6 sessions lasting an hour in the globe. The luminance of the globe, measured in its interior, was 10 foot candles, ± 2 per cent. For 30 trials of 8 sec. duration, spaced at random within each session, the luminance was raised to 73·8 foot candles, ± 2 per cent. If the animal pressed the lever 5 or more times during any such 8 sec. period of increased luminance, it was rewarded with one 0·5 gm. pellet of Purina chow passed automatically down the food chute. Only one pellet was made available, irrespective of the number of presses greater than 5, so that the maximum number of rewards on any one day was 30. Criterion performance consisted in (*a*) obtaining at least 81 out of a maximum of 90 rewards on three successive test days, *and* (*b*) pressing the lever below an average rate of four times per min. during the periods of 10 foot candle luminance on three successive days. Supplementary food (about 30 gm. Purina chow, 10 gm. shelled peanuts, 36 gm. orange) was supplied after each test session. This phase of training lasted 2½–3½ months.

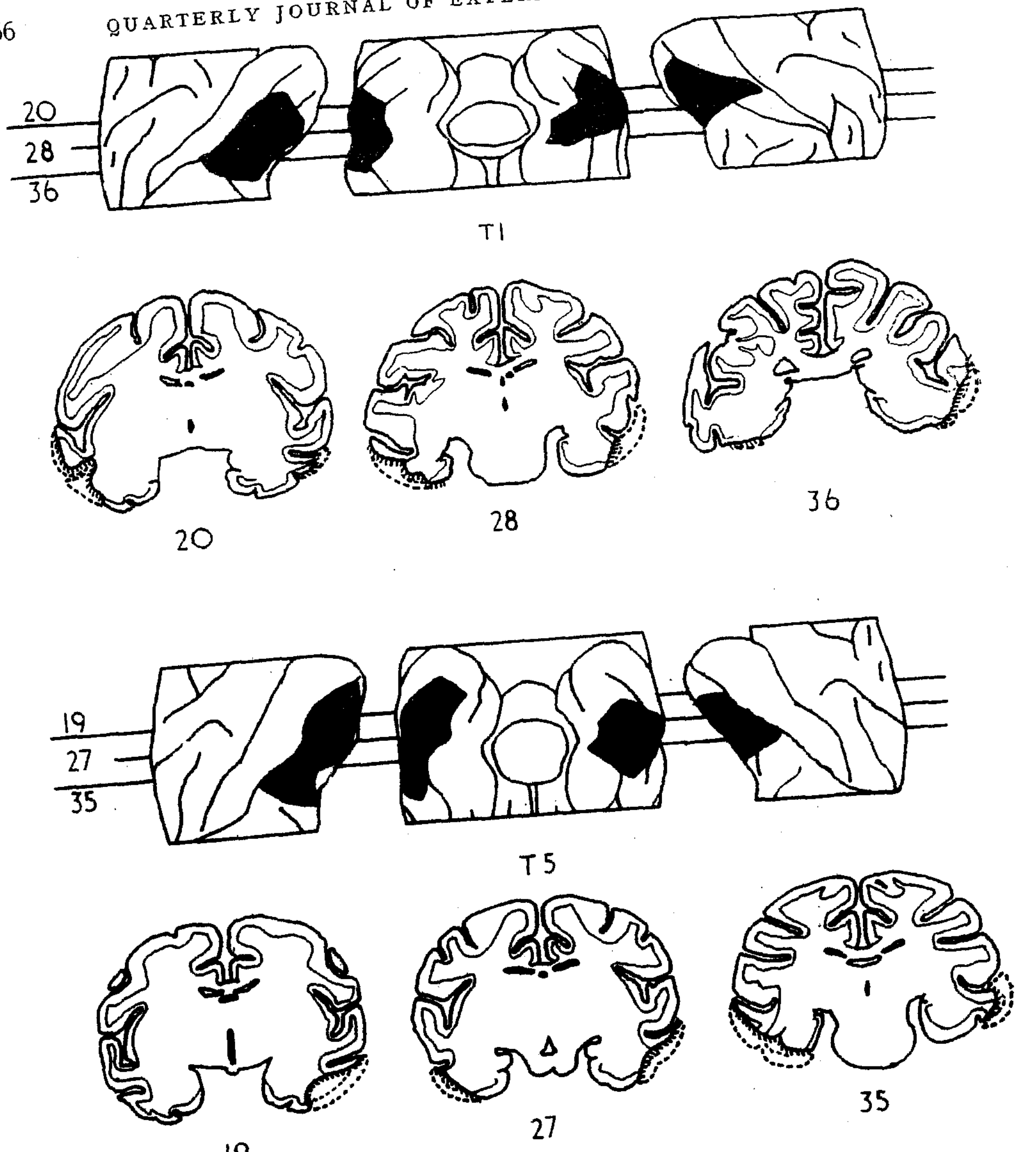

FIGURE 1

Reconstruction of the brains of animals T_1 and T_5, together with representative cross sections through areas of cortical damage. Black indicates the extent of the cortical removals on the surface views.

First pre-operative parametric run. After reaching criterion all four animals were immediately started on the first pre-operative parametric run in which the brightness difference was progressively diminished after each group of four test sessions (method of serial groups). During each daily session of one hour in the globe the overall luminance was still increased on 30 trials of 8 sec. duration to 73·8 foot candles, ± 2 per cent. The intervals between these 30 trials were randomly varied, but averaged 2 min. in duration. During the remaining 56 min. of each session the luminance of the globes was at a given level below 73·8 foot candles and was maintained constant for the four test sessions constituting a step. Thus for the first 4 days (step 1) the difference between the 8 sec.

positive cues (at 73·8 foot candles) and the 2 min. negative cues was 71·1 per cent. of the positive cue; on the next 4 days (step 2) the difference was 35·5 per cent.; for step 3 it was 17·7 per cent.: then 8·8 per cent.; for step 5 it was 4·4 per cent. and finally (step 6) 2·2 per cent. In every case a pellet of chow was provided as reward if the monkey pressed the lever 5 times within the 8 sec. period of the higher level of globe luminance. In order to avoid extinction of the habit as the brightness difference was diminished to below the animals' capacity, the series was terminated whenever *either* (*a*) an animal failed to obtain 40 rewards out of the maximum of 120 possible during any step, *or* (*b*) the ratio of the rate of lever pressing during the total exposure of the positive cue to the rate during the total exposure of the negative cue on any step, fell below 3. After failing to meet this criterion an animal immediately reverted to the conditions of step 1 for 4 days.

Pre-operative learning of pattern discrimination. Following completion of the first parametric run animals T_1 and T_2 were taught to discriminate between two patterns in the Wisconsin General Testing Apparatus. The positive cue was a yellow outline square ($1\frac{3}{4}$ in. by $1\frac{3}{4}$ in. with sides $\frac{3}{8}$ in. wide) painted on a grey ground. A yellow cross ($1\frac{3}{4}$ in. across, $\frac{7}{16}$ in. thick), likewise on grey, served as negative cue. Both cues were painted on the horizontally placed lids of food containers set 12 in. apart. Thirty trials were given each day, using a Gellerman schedule for random left/right positioning of the positive cue, a reward of half a peanut and a non-correction technique. The criterion for acquisition of this discrimination was 90 correct choices in 100 successive trials.

Second pre-operative parametric run. Animals T_1 and T_2 were given a second pre-operative parametric run, 14 days after learning the pattern discrimination in the case of the former, 14 days after completing the first parametric run in the case of the latter. Both started with step 1 and continued according to the procedure of the first run, reverting after failure once more to step 1.

Pre-operative retention of pattern discrimination. Immediately after completing the second pre-operative parametric run animal T_1 was retrained on the pattern discrimination according to the procedure and criterion of original learning.

Operations. Animal T_1 was operated on after relearning the pattern discrimination; animal T_2 after the second pre-operative parametric run, and T_4 as soon as the first pre-operative run was completed. Animal T_3 died following surgery, having completed one pre-operative parametric run and learnt the pattern discrimination.

First post-operative parametric run. Fourteen days were allowed for post-operative recovery and then all three surviving animals were tested on the first post-operative parametric run. The procedure was the same as for the pre-operative runs (no initial post-operative training to criterion), except that animals T_1 and T4 required some help during the first session of step 1, but not thereafter. This help consisted in operating the lever not more than 20 times in all from outside the box during periods of higher luminance.

Post-operative retention of pattern discrimination. Animal T_1 was retrained on the pattern discrimination after competing the first post-operative parametric run.

Post-operative criterion training. Animals T_2 and T_4 were retrained to criterion on the successive overall brightness discrimination after completion of the first post-operative parametric run. The luminance levels and double criterion were the same as required immediately before the first pre-operative parametric run. This phase lasted 3–4 days.

Second post-operative parametric run. Immediately after attaining criterion animals T_2 and T_4 were tested on the second post-operative parametric run. The procedure was the same as on previous runs.

Initial post-operative learning of pattern discrimination. Animal T_4 was taught the pattern discrimination when the second post-operative parametric run had been completed.

Results for Experiment 1

In Table I are presented the thresholds attained by the animals on the successive overall brightness discrimination. It will be seen that the four animals failed to meet the double criterion on the first pre-operative parametric run when the difference in luminance between the positive and negative cues fell to within 8·8–2·2 per cent. of the luminance of the constant (positive) cue. Both pre-operative retest values (animals T_1 and T_2) fall within the same range although the terminal threshold of animal T_2 is improved. Following operation, the three values for the first and the two thresholds for the second post-operative parametric run still fall within the pre-operative range. However, two of the three thresholds on the first post-operative run (animals T_2 and T_4) are raised by comparison with the last preceding pre-operative values for the same animals.

More detailed results for the same test are shown graphically in Figure 2 for animals T_1, T_2 and T_4. Along the abscissa in each graph are plotted steps representing decreasing differences in luminance between the variable (negative) and constant (positive) cues. The values of these differences, expressed as percentages of the luminance of the constant cue, have already been given above for each step. A logarithmic transformation of the most suitable measure of performance is plotted along the ordinate in each graph. This measure is the ratio of the rate of lever pressing (per unit time) during the 16 min. total exposure time of the positive cue on 4 days to the rate of pressing (per unit time) during the 224 min. total exposure time of the negative cue on 4 days. A proportional measure was made necessary by the tendency of some animals to maintain a high rate of pressing even during exposure of the negative cue on the more difficult steps of a parametric run. The logarithmic transformation improves the distribution of the ratio values. The range of pre-operative performance by all four animals is indicated (by shading) on each graph, in addition to the individual scores on all runs of each surviving animal.

Performance during the second pre-operative parametric run is found to be partly inferior in the case of animal T_1 and consistently inferior in the case of animal T_2 to performance on the first pre-operative run. Animal T_2 graduated from step 5 to step 6 on the second run not because its performance was more highly differentiated in respect of the exposure of positive and negative cues than on the first run; rather, the total number of lever presses was increased to 2,569 as against 320 on the first run, and accordingly the number of rewards to 53 as against 10, so that criterion (*a*) (at least 40 rewards on any step) was achieved. It is also noteworthy that the scores on the second post-operative run of animal T_2 (but not of T_4) are again consistently worse than on the first post-operative run. There is then some evidence for progressively deteriorating performance on successive runs even with a constant neurological status.

In comparing the pre-operative with the post-operative ratios, all post-operative scores (excepting only those of animal T_1 on step 1 and of animal T_2 on step 2) are found to fall within the pre-operative range of performance. Only in the case of animal T_4 is the first post-operative run consistently inferior to the preceding pre-operative run. However, not even in this instance can the deteriorated performance be confidently atrributed to the changed neurological status. For only on step 4 is the initial post-operative performance decrement of animal T_4 greater than the deterioration occurring in the case of animal T_2 on the second of two *pre-operative* runs. Moreover the ratio for the second post-operative run of animal T_4 is higher on step 4 than on the pre-operative run. It may therefore be concluded that the three temporal operates are not reliably impaired as compared with pre-test performance at successive brightness discrimination under the conditions of testing of Experiment 1.

Reference must be made to animal T_5 of Experiment 2 in considering the performance of animals T_1 and T_4 on the pattern discrimination. From Tables I and II it will be seen that the range of trials to criterion for the pre-operative learning of this test by the three relatively experienced animals T_1, T_3 and T_5 is 150–280 trials. The post-operative learning score (510 trials) of the equally sophisticated animal T_4 therefore falls well outside the relevant control range (and barely overlaps with the range of 200–510 trials established by the author for six other unoperated and naive animals

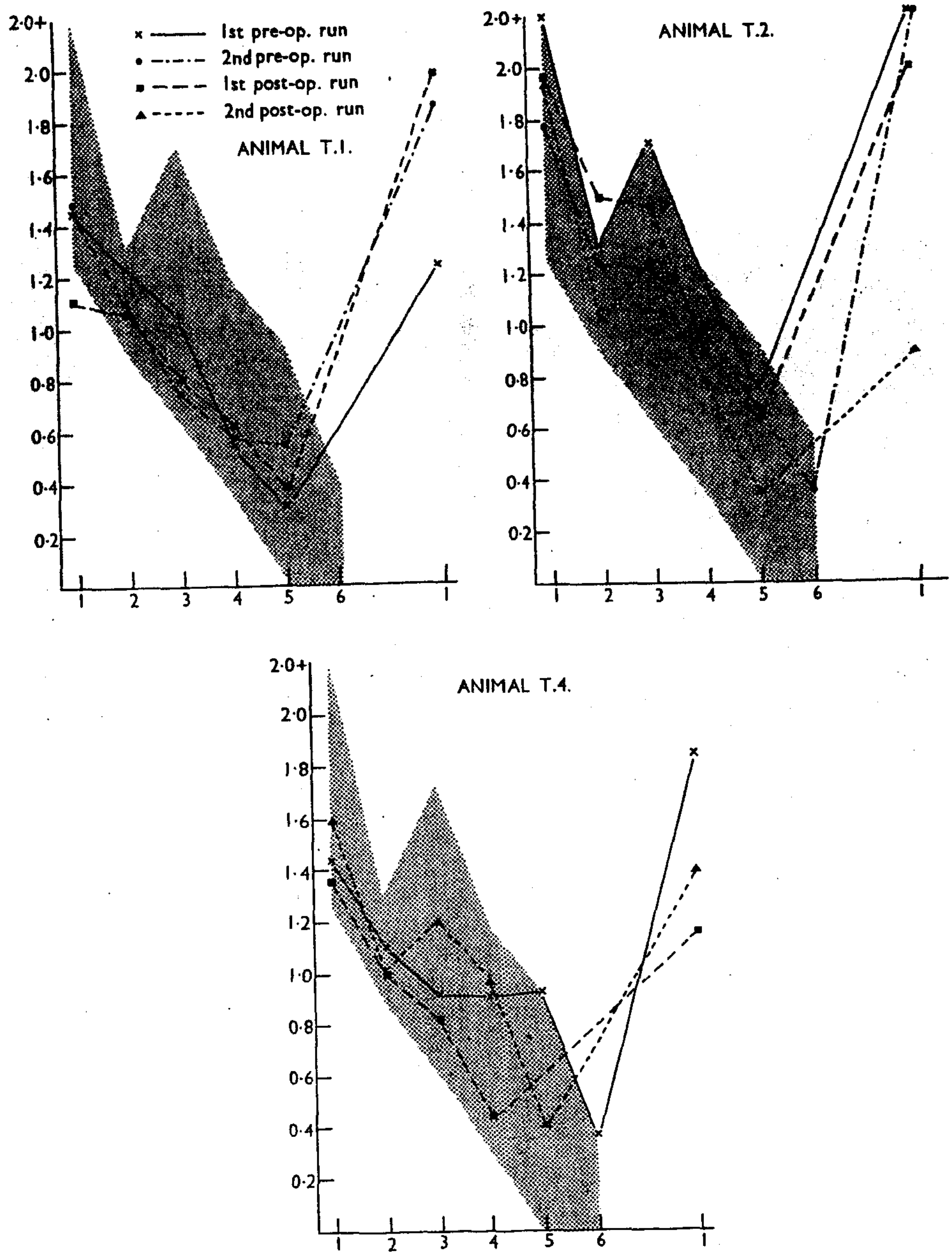

FIGURE 2

Pre- and post-operative performance scores for animals T_1, T_2 and T_4. Steps, representing geometrically decreasing differences in luminance between the positive and negative cues, are plotted along the abscissa. The logarithm of the ratio of the rate of responding during exposure of the positive cue to the rate during exposure of the negative cue is plotted along the ordinate. The range of pre-operative performance by all four animals (T_1–T_4) is indicated by shading.

on the same discrimination). Both animals T_1 and T_5 relearnt the pattern discrimination in 0 trials pre-operatively (i.e. 10 or less errors in the first 100 trials). Animal T_1 was therefore unequivocally (although mildly) impaired following surgery in view of the 190 trials required to regain criterion. Both of the animals (T_1 and T_4) tested on the simultaneous pattern discrimination thus gave evidence of post-operative impairment on this test, whereas they scored within the pre-operative range on the successive overall brightness discrimination.

TABLE I

Training Procedure and Results for Experiment I.

Animals	T_1	T_2	T_3	T_4
	Pre-operative criterion training			
First pre-operative parametric run (minimum luminance difference discriminated) ..	4·4%	4·4%	8·8%	2·2%
Pre-operative learning of pattern discrimination (trials to criterion)	250 (14 days)	— (14 days)	280	—
Second pre-operative parametric run.. ..	4·4%	2·2%	—	—
Pre-operative retention of pattern discimination	0	—	—	—
	Operation (14 days)			
First post-operative parametric run	4·4%	4·4%	Died	8·8%
Post-operative retention of pattern discrimination	190	—		—
	Post-operative criterion training			
Second post-operative parametric run ..		4·4%		4·4%
Post-operative learning of pattern discrimination				510

— Indicates that this stage of training was omitted, so that the animal at once progressed to the next stage except where 14 days' rest intervened.

Experiment 2

Training procedure (*see Table II*)

Pre-operative criterion training. Animals T_5 and T_6 were first trained to criterion (in the same apparatus as for Experiment I) on a successive brightness discrimination where a homogeneous field and an incremental disc of light superimposed upon the field served as alternative cues. Five to six sessions lasting an hour were given each week. The luminance of the globe was 10 foot candles, ± 2 per cent. For 30 trials of 8 sec. duration, spaced at random within each session, a disc of light measuring $\frac{9}{32}$ in. in diameter was projected on to the globe at a height of $10\frac{1}{2}$ in. vertically above the lever. The luminance of the disc was calculated to be 75·1 foot candles on the interior surface of the globe. If the animal pressed the lever 5 or more times during such an 8 sec. period of incremental stimulation it was rewarded with one 0·5 gm. pellet of chow. Criterion performance consisted in (*a*) obtaining at least 60 out of a maximum of 90 possible rewards on three successive test days, *and* (*b*) pressing the lever below an average rate of 12 times per min. during the periods of homogeneous field illumination on three successive days. This phase of training lasted 4–5 months.

First pre-operative incremental cue sampling. After achieving criterion the test conditions remained unchanged for both animals during the following 4 days. This 4 day period was thought to provide a representative sample of initial post-criterion performance on this test.

Pre-operative learning of pattern discrimination. Animal T_5 was then taught the pattern discrimination under the same conditions as in Experiment I.

Second pre-operative cue sampling. An interval of 14 days' rest was allowed to animal T_5 after learning the pattern discrimination and to T_6 after the first sampling period. Both animals were then given a further 4 day sampling period. The test conditions remained the same as for pre-operative criterion training.

Pre-operative retention of pattern discrimination. Animal T_5 was retrained on the pattern discrimination after completing the second pre-operative sampling period.

Operations. Animal T_5 came to operation at once after relearning the pattern discrimination, and T_6 after the second pre-operative sampling period.

First post-operative incremental cue sampling. When 14 days had elapsed to allow for recovery from the immediate effects of surgery both animals were tested in the globe for 4 days under the conditions used for pre-operative criterion training.

Post-operative retention of pattern discrimination. Animal T_5 was retrained on the pattern discrimination after completing the first post-operative sampling period.

Post-operative criterion training. Following retraining on the pattern discrimination animal T_5 was retrained to criterion on the incremental brightness discrimination under the conditions of pre-operative criterion training. This animal required 4 days to meet the criterion. Animal T_6 failed to re-attain the criterion under the same test conditions within 30 sessions.

Second post-operative incremental cue sampling. A final 4 day sample of performance was taken for animal T_5 as soon as it had attained the criterion. Sessions 26–30 of the post-operative period of criterion training were counted as an equivalent sampling period for animal T_6 (although T_6 had failed to meet the criterion).

TABLE II

TRAINING PROCEDURE AND RESULTS FOR EXPERIMENT II

Animals	T_5	T_6
	Pre-operative criterion training	
First pre-operative incremental cue sampling (ratio of response rates to positive and negative cues) . .	6·26	5·28
Pre-operative learning of pattern discrimination (trials to criterion)	150 (14 days)	— (14 days)
Second pre-operative incremental cue sampling . .	5·06	4·94
Pre-operative retention of pattern discrimination . .	0	—
	OPERATION (14 days)	
First post-operative incremental cue sampling . .	5·36	3·01
Post-operative retention of pattern discrimination	210	—
	Post-operative criterion training	
Second post-operative incremental cue sampling . .	5·46	2·18

The symbol — has the same meaning as in Table I.

Results for Experiment 2

In Table II are presented the ratios of the rate of lever pressing during the 16 min. total exposure time of the incremental light disc (positive cue) on 4 days to the rate of pressing during the 224 min. total exposure time of the homogeneous field (negative cue) on 4 days. It is noteworthy that the second pre-operative sample is inferior to the first for both animals.

Animal T_5 gives evidence of improved performance following surgery relative to both its second pre-operative sample and to the two pre-operative samples of animal T_6. On the other hand the performance of animal T_6 declines progressively with continued testing from the level attained during pre-operative criterion training. Thus both pre- and post-operatively the second sample is inferior to the first, so that the decrement apparent on the first post-operative sample cannot be attributed to the surgical procedures with any certainty. Neither temporal operate is therefore unequivocally impaired as a result of surgery on the successive brightness discrimination requiring selective response to an incremental light exposure. On the other hand animal T_5 shows no saving in relearning the pattern discrimination post-operatively.

Discussion

In what way then does the dissociation between the performance of operated monkeys on the present two forms of successive brightness discrimination (no deficit) and on the simultaneous pattern discrimination (deficit) clarify the nature of the defect following bilateral inferior temporal lesions? Taking the impairment of simultaneous pattern discrimination first, the apparent mildness of the post-operative deficit is the only unexpected feature. However, when the mean of the learning scores (227 trials) and their range (150–280 trials) for the present three animals is compared with the mean (358 trials) and range (200–510 trials) for six other unoperated animals trained by the author on the same discrimination but without prior testing in the globe, it is seen that previous experience with the successive brightness discrimination has markedly improved the pre-operative performance on the pattern discrimination. The post-operative deficits on this test cannot therefore be expected to be as severe as in naive animals (cf. Mishkin and Hall, 1955, for scores similar to those of T_4 on initial post-operative pattern learning following size discrimination; and Pribram and Mishkin, 1955, for perfect post-operative retention on a simultaneous pattern discrimination following successive presentation of the same cues).

Turning now to the tests of brightness discrimination, it is true that neither Klüver (1937) nor Settlage (1939) found any loss of capacity to discriminate brightness differences in monkeys with unilateral or bilateral occipital lesions when some loss might have been expected. On the other hand Mishkin and Pribram (1954) using cues differing in reflectivity rather than luminance and the simultaneous two-choice procedure reported defective brightness discrimination after bilateral temporal lesions in baboons. Wegener (unpublished observations) has found a similar impairment in monkeys following bilateral ablation of the temporo-parieto-preoccipital region. In his study the alternative cues (either light sources or illuminated surfaces) were presented successively in one test, simultaneously in another. According to the criterion of number of sessions required for learning as well as by other standards both forms of the brightness discrimination were considerably more difficult for all animals than was the pattern discrimination. Moreover on all runs animals graduated to progressively smaller luminance difference (which could be diminished to as little as 1·1 per cent.) until the discrimination became so difficult that their efficiency was reduced. Therefore successful performance on the brightness discrimination by the temporal operates cannot be plausibly related to either the specific character of the alternative cues nor to insufficient test difficulty.

In evaluating the rôle of differences in cue presentation and response availability it is of importance that Pribram and Mishkin (1955) reported temporal operates to be at least as severely impaired on a successive as on a simultaneous pattern discrimination. The sequential presentation of positive and negative cues in the present study cannot therefore be critical for successful post-operative performance. It is true that in Experiment 1 changes in the "ground" (as used in Gestalt terminology) served as cues for differential responding, whereas in previous studies leading to impaired performance, as well as in the present pattern discrimination, the alternative cues were "figures" set against a ground (of greater or lesser complexity). Nevertheless the temporal lobe defect cannot be related exclusively to "figure" differentiation. For the positive cue in Experiment 2 (in which temporal removals were not followed by impairment) was a disc of light superimposed upon a homogeneous ground.

Is the availability to the animal of a single manipulandum throughout a whole test session the aspect of the test conditions leading to successful post-operative performance at brightness discrimination? In the successive discrimination of Pribram and Mishkin (1955) the formal response ("go and open food cup") was required of the animal whenever the positive cue was presented. This response was not available to the animal in between trials. If it was made in the presence of the negative cue no further reward was forthcoming (i.e. the positive cue was withheld) until the animal ceased responding in this manner on one of successive presentations of the negative cue (re-run correction technique). This procedure served to restrict the formal correct response to trials in which the positive cue was visible. In the present study, however, the animal was in no way penalized for pressing the lever during the long exposure periods of the negative cue. This kind of test situation has been recently discussed by Weiskrantz (1957). Lacking any penalty, most animals progressively increased their rate of lever pressing during the exposure of the negative cue, and this accounts for the deterioration of performance on successive runs and samples. At the same time it might appear that bilateral ablation of the inferior temporal region failed to disrupt a visual discrimination in which the formal correct response is not sharply differentiated by the test conditions from alternative modes of behaviour. Looked at in a slightly different way, the animal had less need to remember before and after operation what responses *not* to make in relation to given cues than in the more traditional forms of discrimination. In the pattern discrimination the animal was, of course, penalized by lack of reward if it made the otherwise correct formal response ("remove lid") in relation to the negative cue.

On the other hand it can be argued (Weiskrantz, personal communication) that the good post-operative brightness discrimination by the temporal operates is the result of prolonged pre-operative training. This view derives support from the recent findings of Chow and Orbach (1957) and of Orbach and Fantz (1958). These latter authors have shown that pre-operative overtraining on an easy discrimination eliminates the impairment that follows temporal ablations in the absence of overtraining. However, the results of Pribram and Mishkin (1955), Mishkin and Hall (1955) and of Pasik *et al* (1957) are at variance with this interpretation. For considerable pre- or post-operative experience of a discrimination served in these studies to abolish the post-operative impairment of temporal animals only on the easy but not on the difficult forms of the tests.

The present results, if confirmed by repetition, would then tend to suggest that the demonstration of a visual impairment in temporal operates is limited to certain conditions of testing. It could no longer be supposed that temporal lesions directly interfere with the visual "input" upon which discrimination behaviour is based (an interpretation rejected by Pribram and Mishkin, 1955, although still left open by their findings). For not only has a change in the "situational" variables (to use their term) affected post-operative performance in the present study out of all proportion to the difference in the cues employed in brightness and pattern discrimination; but moreover no reliable impairment has been found on the brightness discriminations despite their greater difficulty. Instead, emphasis has fallen on the test conditions relating to either the amount of pre-operative training or to response differentiation. It might be predicted, if the availability of a single manipulandum is the crucial factor, that temporal operates would be impaired under the same conditions of cue presentation as used in Experiment 1, providing that two levers were made available, the one serving to procure reward at a high level of ground luminance, the other at a lower level. At any rate the present results might tentatively be taken to confirm the view of Klüver (1937) that "in future studies of cortical cases it may seem worthwhile to study more thoroughly the rôle of the motor components in visual reactions."

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