# VENTRAL TEMPORAL LOBE LESIONS AND VISUAL ODDITY PERFORMANCE

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(Accepted January 31st, 1971)

## INTRODUCTION

It has been established for a number of years that bilateral ablation of the inferotemporal cortex (middle and inferior gyri of the temporal lobe) in the monkey severely impairs the learning and retention of visual problems involving the discrimination of pairs of objects, colour or form stimuli. There are several possible explanations for this impairment, two of which are clearly distinct. The monkey may fail to choose the correct stimulus in the discrimination task either because he cannot see the difference between the stimuli or because he cannot remember which stimulus is rewarded. When the impairment was first described in any detail by Chow[2] the findings were discussed in the context of a clinical syndrome, termed visual agnosia, and it was suggested that the inferotemporal impairment in the monkey reflected a visual associative disorder retarding the ability of the animal to remember from trial to trial which of the stimuli was consistently associated with reward. More recently, it has been demonstrated that the lesion also changes the way in which component parts of complex visual stimuli are attended to and categorised[1,5], and it has been suggested that a perceptual disorder of this kind could be responsible for the range of discrimination and learning deficits associated with the inferotemporal lesion.

It is reasonable to suppose that perceptual processes precede associative mechanisms and in the circumstances it would appear appropriate to suggest that the impairment of associative learning in the inferotemporal is a result of impaired perception and does not reflect an independent disorder. Despite the simplicity and attractiveness of such a unitary perceptual hypothesis, its acceptance has depended on the demonstration of a perceptual disorder independent of any memory impairment.

In practical terms it is difficult to design for the monkey an experiment which dissociates the two functions. What is needed ideally is, on the one hand, a test of perceptual discrimination which does not require associative memory, and, on the other, a test for visual associative memory which does not require perceptual discrimination. In an attempt to achieve the first objective a variant of the 'oddity problem' devised by Harlow[7] has been used in the present study.

The monkey was presented with an array of 4 panels displaying visual stimuli, 3 of which were the same and one different, and was reinforced for pressing the panel displaying the odd stimulus. In oddity discrimination, unlike conventional two-choice problems, the necessity for trial to trial memory of the specific characteristics of the correct stimulus is excluded because all the relevant information is present at the time the choice is made. To succeed in this task the animal first learns the principle of responding to the odd stimulus of the array and will then respond correctly on any trial provided the principle is retained and the stimuli are discriminable. The rationale of the present experiment was to superimpose on the oddity principle visual discriminations of varying perceptual difficulty. The task is not, however, as purely perceptual as could be wished, since it requires that the oddity principle itself be remembered. It is important to have independent evidence that the oddity concept has been acquired and this is best achieved by demonstrating rapid transfer to novel problems added to the pre-operative series. In the absence of such evidence the task may be no more than a series of specific discrimination problems[4,8]. Furthermore it is necessary in the case of impaired performance after a brain lesion, to have evidence that the principle has not been lost before it can be concluded that the perceptual difficulty of the discrimination is responsible for the decrement in performance.

The animals were first trained on the oddity principle with a single pair of stimuli. Several other problems were successively introduced and learned to criterion. Pre-operative and post-operative retention of these problems and post-operative learning of new problems were studied.

## MATERIALS AND METHODS

### *Apparatus*

The monkey sat in a transport cage in a dimly illuminated box, facing 4 stimulus panels (8 cm × 9 cm) arranged in a rectangular display on a vertical plate in front of him (Fig. 1). Twelve alternative stimuli, based on Letraset designs, were available from Grason–Stadler read-out projectors mounted directly behind each panel. In front of each panel was a hinged perspex window which, when depressed by light touch, activated a microswitch. Peanut rewards were delivered to a trough directly under the panel to which the correct response had been made. The peanut delivery mechanism made a loud click when operated, and as an additional form of secondary reinforcement the intensity of the houselight in the box was increased after a correct response.

At the start of a trial the four stimulus panels lit up. The monkey then indicated his choice of the odd stimulus by pressing the appropriate panel. Following the response to any panel the stimuli were extinguished and a 10 sec intertrial interval ensued. If the choice was correct, reward was given immediately and, during the inter-trial interval, the box was illuminated by the houselight; if it was incorrect there was no reward and the box was dimmed during the interval. For any particular pair of stimuli the eight possible arrangements of the two stimuli (either one of the two odd in each of the 4 positions) occurred in random order. A non-correction schedule was

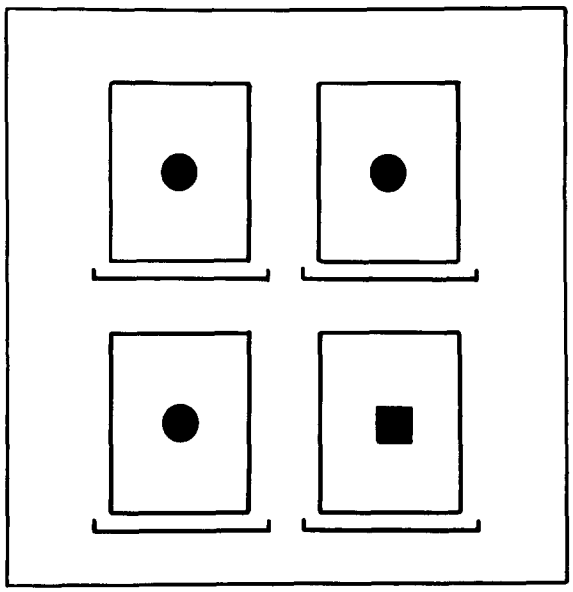

Fig. 1. Diagram of typical stimulus array indicating the relative positions of the 4 response panels with their reinforcement trays directly below.

used in general, but in some subjects it proved necessary to give correction trials. A single testing session contained 100 trials.

*Subjects and surgical procedure*

The subjects were 9 young rhesus monkeys. With the length of pre-operative training matched as far as possible, three were assigned to each lesion group. Three were given bilateral superior collicular lesions (C); 3 bilateral posterior inferotemporal lesions (PT) and 3 bilateral total inferotemporal lesions (LT).

The PT lesion included the anterior bank of the preoccipital sulcus and extended anteriorly to the mid-temporal region and dorsally to include the lower bank of the superior temporal sulcus. The LT lesion had the same posterior and dorsal boundaries but extended considerably more anteriorly into the temporal lobe to include the major part of middle and inferior temporal gyri.

At the completion of the testing programme the animals were killed with Nembutal and the brains prepared for histological processing. The C lesions were studied on stained transverse sections and the extent of the lesion in the PT and LT groups was judged on the basis of surface inspection.

The C lesions were disappointing. In one animal the depth was satisfactory but the main lesion placement was posterior to the superior colliculus. In the remaining animals the lesions were more substantial but rather anterior. On the basis of this information, the C group had better be considered a control group with non-specific midbrain lesions.

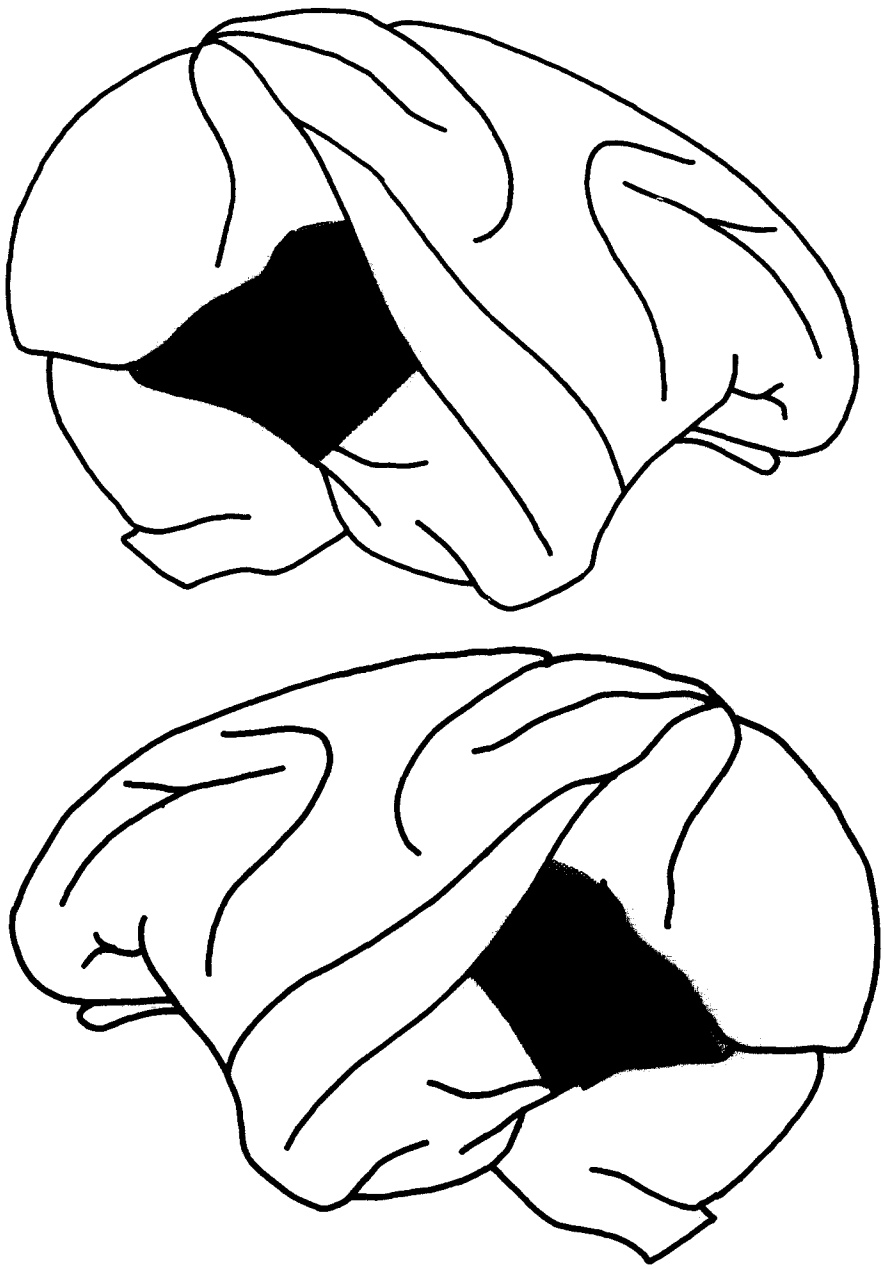

Fig. 2. Lateral views of the left and right hemispheres indicating the minimum (black) and maximum extent (stippled) of the cortical damage in the group PT.

Fig. 2 indicates the minimum and maximum extent of the left and right cortical damage in the PT group. The total lesions in the group LT had the same boundaries but extended considerably further towards the temporal pole.

TABLE I

STIMULUS PAIRS USED IN THE ODDITY TESTING

Numbers and names are those used in referring to pairs in the text.

| | |  | Red<br>Green |  |  |  |  |  | Green<br>Grey |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Star/ square | Hori- zontal/ vertical bar | Open/ filled square | Red/ green circle | Circle/ square | Star I/ star II | Black/ white circle | Large/ small circle | Light/ dark- grey circle | Green/ grey circle | Square/ bar |
| Problem | | | | | | | | | | |
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| Training stimulus | | | | | | | | Post-operative only | | |

*Pre-operative training*

Oddity performance was first shaped with the Star/Square stimulus pair. This was done in stages and the actual programme varied for each animal depending on his particular pattern of progress. The criterion level was set at 70% correct in a session of 100 trials (note that chance performance would result in only 25% correct). The training to this level for the first stimulus pair took on average 25 days.

Other stimulus pairs (Table I, 2–9) were then introduced and the animals trained to criterion on each. With these new pairs, training was started immediately at the oddity stage. It had been expected that the oddity principle would be transferred to the new situations and a good level of performance quickly achieved. This proved not always to be so. With certain pairs, *e.g.* Red/Green, Star I/Star II, Open/Filled Square, performance did indeed reach criterion immediately or within a day or two, but with other problems *e.g.* Circle/Square, Light/Dark Grey, performance was initially very poor and only slowly built up to criterion. On one pair, Horizontal/ Vertical Bar, no animal ever scored above chance and this pair was excluded from the series. It was considered at the time that the major goal for this stage of training was to get the animals to criterion on all problems, and the way in which this was done was not altogether standardised. Originally it was intended that the animals should be given the stimulus pairs in the same order and trained to criterion on each successively. When it was found that particular animals had great difficulty with certain pairs it seemed impractical to follow this standard procedure and heuristic modifications were made to the programme, *e.g.*, the introduction of an easy pair before the animal had mastered a difficult one, use of correction trials and so on.

When the animals had reached criterion with all pairs testing was repeated with each pair over again. This time the order of the pairs was standardised (3–9 in Table I), and correction trials were not used. If an animal failed to reach criterion within 100 trials further training was given. Most animals in fact reached criterion on the

first day with every pair except for Light/Dark grey on which they took an average of 3 days. At this stage performance with the easier pairs had reached a high level and scores on the first day were in several cases well over 90% with an average response latency of under 2 sec.

When the animal had reached criterion for the second time with each pair, pre-operative training was complete and two weeks were allowed to elapse before surgery was performed.

*Post-operative testing*

Testing was resumed one week after operation. The same stimulus pairs were given in the same order as prior to the operation but with the addition of two new pairs at the end to test for retention of the oddity principle (Table I, 10–11). Each pair was tested for 3 successive days and when all the pairs had been presented once in this manner the series was started again. A further 3 days were given with each pair, but this time eliminating any pairs on which the animal had reached criterion on the previous run. Thus the series re-cycled, getting progressively shorter as criterion was reached with one pair after another. It was decided to give a maximum of 12 more

TABLE II

POST-OPERATIVE RETENTION AND NEW LEARNING

Upper figures for each subject represent errors to achieve criterion on each problem after first criterion has been reached*. Lower figures indicate the total errors to learn each problem including the training which preceded the first criterion. A + indicates that criterion was not reached with the limits of testing.

| | | □ ■ | Red Green | ● ■ | ✪ ✪ | ⊙ ● | ● ● | ◍ ◍ | Green Grey | ■ — |
|---|---|---|---|---|---|---|---|---|---|---|
| C | $A_2$ | * | 4 | 4 | 9 | 30 | 20 | 141 | 3 | 6 |
| | | 8 | 4 | 4 | 9 | 30 | 20 | 141 | 3 | 6 |
| | $N_3$ | * | 2 | 8 | 7 | 11 | 60 | 22 | 6 | 3 |
| | | 6 | 2 | 8 | 7 | 11 | 60 | 22 | 6 | 3 |
| | $N_2$ | * | 5 | 29 | 3 | 21 | 17 | 257 | 21 | 0 |
| | | 5 | 5 | 29 | 3 | 21 | 17 | 257 | 21 | 0 |
| LT | $A_1$ | 99 | 10 | 848+ | 163 | 23 | 450 | 246 | 21 | * |
| | | 323 | 196 | 1078 | 345 | 182 | 618 | 405 | 176 | 91 |
| | $N_1$ | * | 118 | 767+ | 27 | 182 | 104 | 529 | 174 | 13 |
| | | 206 | 320 | 978 | 195 | 382 | 283 | 739 | 383 | 138 |
| | $C_1$ | 24 | 401 | 826+ | 43 | 170 | 204 | 438 | 298 | * |
| | | 428 | 829 | 1251 | 440 | 572 | 630 | 874 | 704 | 291 |
| PT | $B_1$ | 7 | * | 449 | 58 | 102 | 226 | 162 | 22 | 16 |
| | | 192 | 79 | 449 | 58 | 102 | 226 | 162 | 22 | 16 |
| | $C_2$ | * | 21 | 307 | 15 | 16 | 14 | 252 | 6 | 13 |
| | | 122 | 21 | 307 | 15 | 16 | 14 | 252 | 6 | 13 |
| | $N_4$ | * | 22 | 363 | 8 | 17 | 60 | 30 | 10 | 5 |
| | | 9 | 22 | 363 | 8 | 17 | 60 | 30 | 10 | 5 |

days (4 runs of 3 days) with each pair beyond the time at which the criterion of 70% correct was first achieved for any pair.

*Statistical procedure*

Any group differences on the behavioural measures in the experiment were evaluated by the non parametric Mann–Whitney U-test. Statements of significance thus imply non-overlapping scores ($N = 3$, $U = 0$, $P = 0.05$).

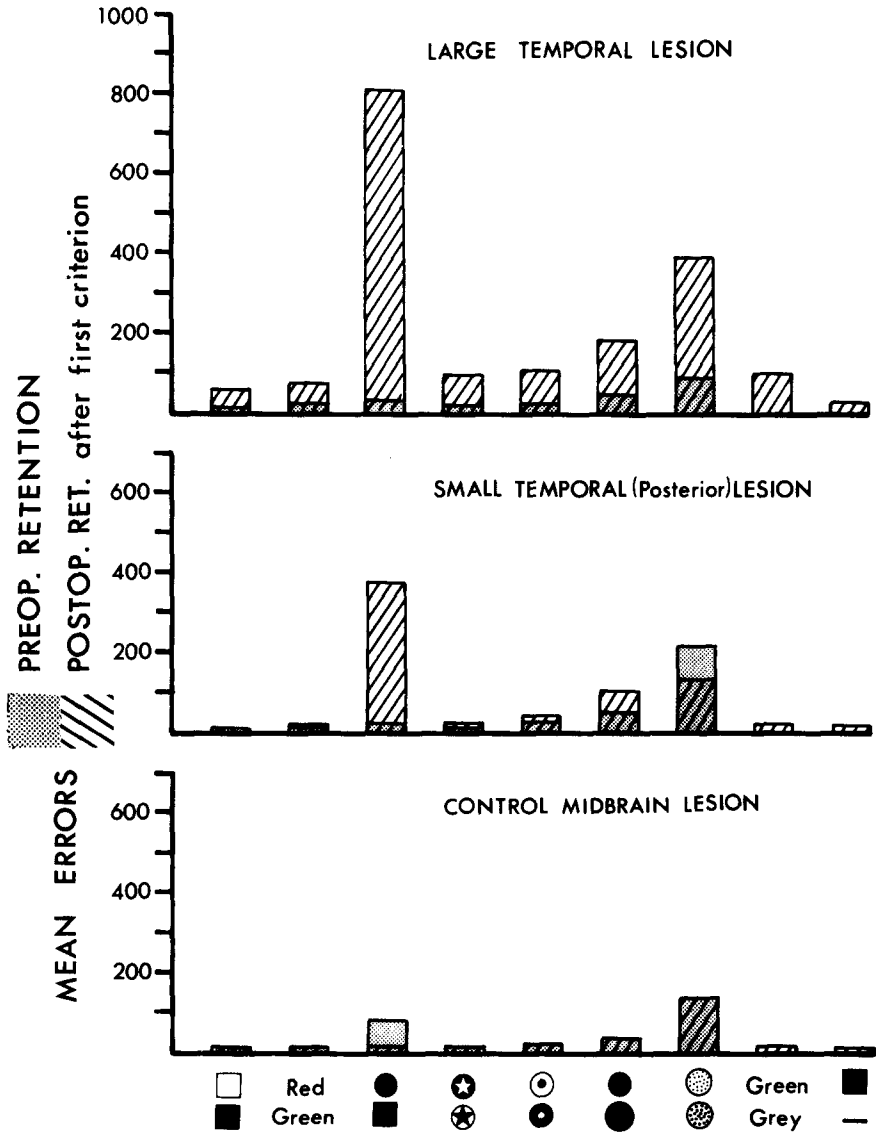


Fig. 3. The mean errors on pre-operative retention compared with the mean errors to relearn these 7 problems post-operatively and to learn two new problems. The post-operative error scores for each animal were calculated after that animal had achieved post-operative oddity performance criterion on one of the problems.

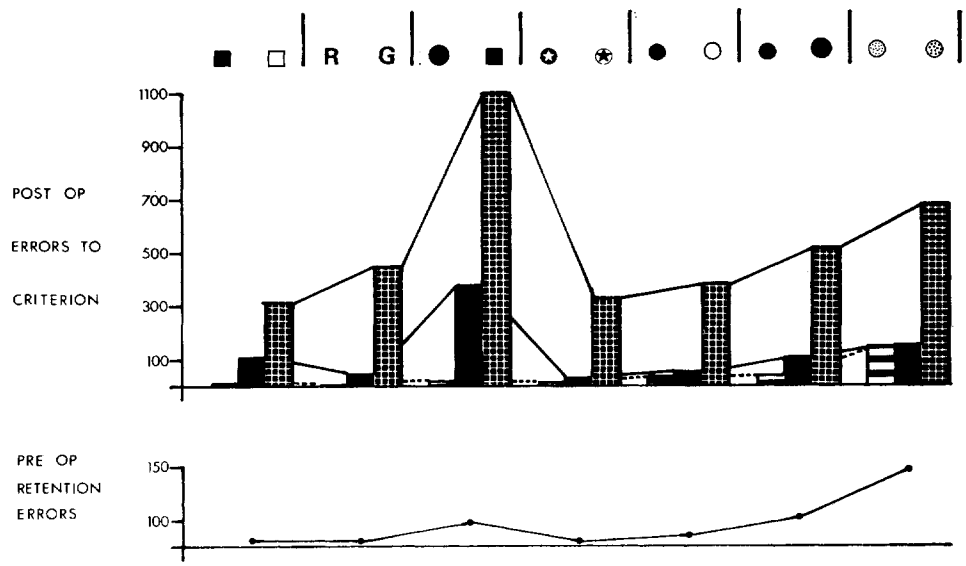


Fig. 4. Mean total errors to reach criterion on the 7 problems tested pre- and post-operatively, compared with the mean pre-operative retention profile. Squares, LT; black, PT; bars, C.

## RESULTS

The post-operative performance of the animals in the 3 lesion groups are presented in Table II in which two scores are given for each subject on each of the problems. The upper row of figures represents the errors to learn the problems after the criterion had been reached for the first time with any pair. Accordingly there is no score for the problem which was learned first and this is indicated by an asterisk. These error scores are averaged and summarised for each experimental group in the histogram of Fig. 3, together with the average pre-operative retention scores on problems 3–9.

The lower row of figures for each animal records the total number of errors to reach criterion on each problem including those up to the point at which criterion was first reached with any pair. In groups C and PT the first or second problem encountered post-operatively was learned to criterion during the initial block of testing session and accordingly the two error scores on the remaining problems are identical. Only in the group LT who were trained for at least 3 sessions on each of the problems of the series (*i.e.* for 27 sessions) before a criterion was reached for the first time are the two scores different. The averaged group data on this second error measure are presented in Fig. 4 together with the pre-operative retention profile.

The difficulty experienced by the group LT in achieving a post-operative oddity criterion is emphasized in Table III which presents the number of daily sessions to reach the first criterion and the number of sessions and errors made during the acquisition of the particular problem which was learned first.

The animals with control midbrain lesions performed well post-operatively, all

TABLE III

LEARNING SCORES TO THE FIRST POST-OPERATIVE CRITERION RUN

| | | *Number of daily sessions to attain first criterion run (criterion session not included)* | *Total number of sessions and errors (including criterion session) to learn the particular problem on which the first criterion was achieved* | |
|---|---|---|---|---|
| | | | *Sessions* | *Errors* |
| C | $A_2$ | 0 | 1 | 8 |
| | $N_3$ | 0 | 1 | 6 |
| | $N_2$ | 0 | 1 | 5 |
| LT | $A_1$ | 26 | 3 | 91 |
| | $N_1$ | 27 | 4 | 206 |
| | $C_1$ | 51 | 7 | 291 |
| PT | $B_1$ | 4 | 2 | 79 |
| | $C_2$ | 2 | 3 | 122 |
| | $N_4$ | 0 | 1 | 9 |

achieving their first criterion during the initial testing session on the □/■ problem (Table III). This performance was sustained and all reached criterion on 5 of the other problems, including those two introduced for the first time post-operatively (Table I, 10–11), during the first training session on those problems. Retention of the remaining discriminations required more training but the overall profile of performance was similar to that of the pre-operative retention profile, indicating that the problems represented a valid and stable spectrum of difficulty.

The group PT was slightly but significantly impaired in the reattainment of the oddity principle post-operatively, and required more training than the controls to achieve 70% performance for the first time (Table III). However once this criterion had been reached they learned the remaining problems, except for the form (●/■) discrimination, with scores not significantly different from those of the control animals.

The animals with large temporal lesions showed a severe impairment in re-attaining oddity performance. Consequently in terms of total errors to learn, the group LT was significantly impaired both with respect to the controls and the group PT on every problem. However, once this criterion was achieved the LT animals eventually learned the remaining problems to criterion, except for the form discrimination. Their impairment was impressively larger than in the PT group, although it showed the same general profile (Fig. 4).

## DISCUSSION

The superior colliculus lesions were not satisfactory and this study cannot claim to substantiate early reports that such lesions do not impair discrimination performance[9]. This group of animals is therefore considered to be a control midbrain lesion group.

The two inferotemporal groups showed similar patterns of impairment, although the defects of the LT group were in all respects more severe than those of the PT group. In both groups there was an initial failure to retain the oddity principle and a subsequent selective defect on the form problem after the principle had been relearned. The loss of the oddity principle which was, however, transient in the PT group might be considered compatible with recent reports that selective lesions to the anterior inferotemporal cortex result in deficits on complex visual learning tasks[3,6]. In addition the selective defect on form discrimination, occurring as it did at a stage when there should have been no need to remember the specific stimuli from trial to trial, strongly suggests that perceptual classification as such was impaired in these animals. The selectivity of the perceptual defect was made most conspicuous in the PT group on account of the relatively unimpaired oddity performance.

SUMMARY

Monkeys were trained pre-operatively on a range of visual oddity discrimination tasks. Large inferotemporal (LT) lesions resulted in severely impaired oddity performance, but even when the concept had been reattained the relearning scores were related to the perceptual difficulty of the individual tasks, particularly in the case of the form discrimination. Smaller lesions to the posterior segment of the inferotemporal region (PT) resulted in only a slight loss of oddity performance as such but a severe impairment on the form problem. Thus in contrast to the group LT, post-operative performance in the group PT was clearly influenced primarily by the perceptual nature of the discrimination.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the help and interest of Professor L. Weiskrantz in this work and encouragement and research facilities made available by Professor O. L. Zangwill.

The work was supported by a grant from the Medical Research Council (968/96/B) and a Science Research Council training scholarship to the second author.

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