Elevation of Visual Pattern Discrimination Limen in Monkeys with Total Removal of Inferotemporal Cortex

Eiichi IWAI, Yasutaka OSAWA, and Yoshitomo UMITSU

Department of Behavioral Physiology, Tokyo Metropolitan Institute for Neurosciences, Tokyo, 183 Japan

Abstract Attempts were made to test the validity of the general view that inferotemporal lesions in monkeys do not result in a visual acuity disorder. It was found in the first experiment that monkeys with total removal of the inferotemporal visual area (TIT monkeys) showed a significant elevation of the discrimination limen for visual patterns of reduced sizes even when compared to monkeys with removal of lateral striate cortex (LS monkeys); yet in a food-morsel (raisin) detection test the TIT monkeys performed as well as normal monkeys, although the LS monkeys showed significant deficits. A second experiment was conducted, in which the same subjects were tested with the same patterns as in the first experiment but with the stimulus background changed from the square used earlier to an enlarged disc. While both normal and LS monkeys performed this task easily, the TIT monkeys could not learn the discrimination within the training limit of 1,200 trials. The results suggest that such a marked elevation of the discrimination limen in the TIT monkeys as found in the first experiment is not attributable to a visual acuity disorder, but is explained as due to an impairment of the pattern perception mechanism.

Bilateral ablations of the inferotemporal cortex of monkeys produce a marked impairment of visual pattern discrimination (cf. reviews by Mishkin, 1966, 1972; Gross, 1973; Weiskrantz, 1974; IWAI, 1978). Most investigators have favored the view that this impairment is due to disruption of some high-level visual function such as pattern perception or learning, but the alternative proposal has also been advanced that the impairment results instead from a loss of a more basic visual sensory function such as visual acuity (Pask et al., 1960; Valciukas and Pasik, 1965). The present study attempted to examine the latter possibility.

IWAI and Mishkin (1968, 1969) demonstrated that the area in the inferotemporal cortex concerned with visually mediated behavior includes both areas TE and PH (or TEO) in the cytoarchitectural charts of Bonin and Bailey (1947).
and Bailey et al. (1950). The inferotemporal visual area newly defined is thus much wider than presumed previously, because only area TE had been considered as the visual area (Chow, 1951; Mishkin, 1954; Mishkin and Pribram, 1954). No one has yet tried to determine whether removal of the total inferotemporal visual area affects visual sensory function. Such an investigation would provide a more sensitive test of the earlier proposal, for a true sensory loss that might go undetected in a monkey with a partial lesion could well become manifest after a complete removal. If impairments were detected by some kinds of visual sensory tests, it would weaken the prevailing view that the inferotemporal cortex is concerned with visual perception or learning.

In order to pursue the above question of whether the inferotemporal cortex is involved in visual sensory function, the first experiment examined the effects of total removal of the inferotemporal visual area (TIT lesion) on performance of two different visual acuity tests. One test was a food-morsel detection test which required detection of a small piece of food. This test is readily performed by normal monkeys, but is sensitive to the loss of visual acuity produced by geniculo-striate damage (Keating and Horel, 1972). The second test, which was based on the visual acuity measure used in the clinic, was to determine a visual discrimination limen for patterns of reduced sizes. If monkeys with TIT lesion (TIT monkeys) showed impairment in both tasks similar to that seen in monkeys with striate lesions, it would be concluded that TIT monkeys suffered an impairment in acuity. As will be described below, the TIT lesion yielded contradictory results in the two tests. A second experiment was therefore performed in an attempt to resolve the contradiction. The same subjects were tested with the same pattern as in the first experiment, but with the stimulus background changed from a square to an enlarged disc.

**EXPERIMENT I**

**Methods**

**Subjects.** Nine experimentally naive monkeys (Macaca mulatta) weighing 3 to 4 kg at the beginning of the experiment were used. They were divided into three groups of three monkeys each, matched on the basis of their preoperative learning scores in the standard pattern discrimination (Table 1). These three groups were then given either a total inferotemporal lesion (TIT group) or a lateral striate lesion (LS group), or kept as unoperated controls (UNOP group).

**Apparatus.** Testing was conducted using a Wisconsin General Testing Apparatus (WGTA) inside a darkened, sound-shielded room. The test tray was placed at the level of the cage floor. The tray used for the food detection test had two painted figures of a raisin, each about 10 mm in diameter, spaced 28 cm apart and 20 cm in front of the vertical bars of the test cage. The food cue was a small, squeezed, and thus relatively thin, raisin of less than 10 mm in diameter.
VISUAL LIMEN IN INFEROTEMPORAL MONKEYS

Standard pattern stimuli

Pair 8/8 or S

Test pattern stimuli

<table>
<thead>
<tr>
<th>Pair 6/8</th>
<th>Pair 4/8</th>
<th>Pair 3/8</th>
<th>Pair 2/8</th>
<th>Pair 0.8/8</th>
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Fig. 1. Patterns used for discrimination. Top, standard patterns used for training. In the second row are shown patterns used for determining discrimination limen. Fractions attached above each pair of patterns indicate sizes relative to that of the standard pattern.

The tray used for the pattern discrimination and the limen test had two foodwells spaced 30 cm apart and 15 cm in front of the bars of the cage. In the pattern discrimination test monkeys were required to discriminate a plus sign (positive) and an outline square (negative) which were made with white paper and pasted on dark-gray cardboard plaques, 7.5 cm × 7.5 cm. The standard pair of patterns, which was used for training, was the plus sign having arms 1.1 cm wide and 6.5 cm long and the outline square having sides 0.9 cm wide and an outside length of 5.0 cm (Fig. 1, S or 8/8). The two patterns were equal in white area. For the limen test, five pairs of pluses and squares were employed (Fig. 1, pairs 6/8 to 0.8/8) which were proportionally reduced in size but displayed in the middle of the dark-gray cardboard plaques of the same size as those used for the standard patterns. The ratios of the five test pairs to the standard (S or 8/8) were 6/8, 4/8, 3/8, 2/8 and 0.8/8, respectively. In the 6/8 pair, for example, the plus sign had arms 0.8 cm wide and 4.8 cm long, and the outline square had sides 0.7 cm wide and an outline length of 3.8 cm.

Testing procedures. Preoperatively, all the subjects were trained for the standard pattern discrimination and then on the raisin detection task. For the latter test, a raisin was placed on one of the two painted spots, its position being chosen in each trial in a predetermined quasirandom manner. Thirty testing trials were conducted a day, in 3 blocks of 10 trials each, and continued until the animals attained the criterion of 10 correct choices in a block of 10 trials. Intertrial intervals, during which a screen was lowered to shut off the subject’s front view, lasted 15 to 25 sec.

Thirty standard pattern discrimination trials were conducted a day by the simultaneous noncorrection method until the animals attained the criterion of 90 correct choices out of 10 consecutive blocks of 10 trials each. In this test, also, a correct response was rewarded with a raisin, whereas an incorrect response was neither rewarded nor punished. The positions of the two stimulus cardboards which were put over the foodwells were interchanged randomly from trial to trial.
Intertrial intervals were again 15 to 25 sec.

The limen test with the patterns of reduced sizes was introduced postoperatively after the animals had relearned the standard discrimination. The threshold was determined by the descending and ascending methods. For each determination, testing started with the standard pair. If the subject failed to make 8 correct choices out of a block of 10 trials, it was retrained with the standard pair until this criterion level was achieved. The descending threshold was then determined by presenting successively smaller pairs until on a given pair the subject failed to attain a criterion score of 8 or more correct responses out of a block of 10 trials within 3 consecutive blocks. On the following day, the ascending limen was determined. After testing with the standard pair, the pair previously determined to be the descending limen was presented. If the subject failed to attain the criterion within 3 blocks of 10 trials each, successively larger pairs were presented until the animal did reach the criterion (ascending limen). The discrimination limen was expressed as the mean of the descending and ascending limens. The procedure was repeated several times over a 2-year period, in order to measure the reliability of the limen and, simultaneously, to detect a possible recovery with training from the elevated discrimination limen shown in the early postoperative period.

Loci and extent of lesions. Brain lesions were made shortly after completion of training for the standard pattern discrimination and examination with the raisin detection test. Animals were anesthetized with hydrochloride ketamine (5–10 mg/kg, i.m.) and sodium pentobarbital (30–34 mg/kg, i.p.), and operations were performed with aseptic techniques. One-stage, bilaterally symmetrical cortical removals were made by aspiration with a small-gauge sucker. For the TIT group, an attempt was made to remove the total inferotemporal visual area defined by IWAI and MISHKIN (1969). The lesion extended dorsoventrally from the superior temporal sulcus, including its inferior bank, to the occipitotemporal sulcus, including its lateral bank, and caudorostrally from the ascending limb of the inferior occipital sulcus, including its anterior bank, forward 2.5 cm to the posterior portion of the anterior middle temporal sulcus. For the LS group, an attempt was made to remove the total lateral striate cortex, which represents the central 6–8° of the visual field according to the estimates of TALBOT and MARSHALL (1941).

After completion of testing, the animals were given a lethal dose of sodium pentobarbital and perfused through the heart with saline and 10% buffered formalin solution, after which the brains were removed and photographed. The brains of monkeys 14, 45, 62 and 70 were embedded in celloidin and sectioned at 30 µm in the frontal plane, while the others were cut at 50 µm with the frozen technique. Every tenth section was stained with thionin, and these sections were used to reconstruct the lesion and to determine the locus, extent and severity of retrograde degeneration in the thalamic nuclei.

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Results

1. Histological results

Lesions. Reconstructions of a representative lesion from each group and cross sections through the lesions are illustrated in Fig. 2. In general, the locus and extent of the lesions conformed to the experimental plan, although occasionally they turned out to be slightly larger than intended. In the TIT group, the main variation was in the extent of damage to the ventromedial border, some of the lesions extending a small distance beyond the occipitotemporal sulcus into the fusiform gyrus. In the LS group, there was sometimes a slight invasion into the ventral OB area beyond the OC-OB border. Also, in Monkey 14 from the TIT group, the posterior half of the lesion on the right side invaded the superior bank of the superior temporal sulcus.

Retrograde thalamic degeneration. The findings on retrograde degeneration in the lateral geniculate (LGN) and pulvinar nuclei are also illustrated in Fig. 2. Severe retrograde cell loss, cell degeneration and gliosis were seen in the LGN of all the monkeys in the LS group, and this degeneration was well localized in the central sector of the posterior half of the LGN to which the foveal and macular areas of the retina project (Malpeli and Baker, 1975). On the other hand, in the TIT monkeys degeneration and gliosis in the LGN were observed only sporadically. This degeneration, slight to moderate in degree and seldom seen in the foveal representation area, presumably resulted from minor damage to the optic radiation.

Retrograde degeneration and gliosis were also seen in the pulvinar nucleus of all the monkeys in both TIT and LS groups. Again, the loci, extent and severity of retrograde changes within the pulvinar following these two lesions were different each other. In the TIT monkeys, moderate or occasionally heavy degeneration and gliosis were well localized in the ventrolateral part of the lateral pulvinar, and slight to moderate changes in the ventrolateral part of the inferior pulvinar and in the caudal part of the pulvinar (caudal pulvinar). On the other hand, in the LS monkeys, slight degeneration and gliosis were seen mainly in the dorsolateral part of the inferior pulvinar, slight or negligible changes in the rostrolateral part of the lateral pulvinar and no degeneration in the caudal pulvinar. No retrograde change was observed in the medial and oral pulvinars of any of the subjects of either the TIT or LS group.

2. Behavioral results

The behavioral results obtained in Experiment I are presented in Table 1, and are summarized in Fig. 4.

Raisin detection. Preoperatively, none of the subjects ever failed to detect the small raisin. Postoperatively, all three monkeys in the LS group (LS monkeys) showed a significant impairment ($p<0.05$, Mann-Whitney U-test; Mann and Whitney, 1947). After a small number of retraining trials, however, they again
Their average score for relearning was 27 trials and 6 errors. On the other hand, 2 out of the 3 TIT monkeys performed perfectly, while the third showed only a slight deficit. The group mean score for relearning was 3 trials and 1 error (p>0.50, U-test). It may be concluded, therefore, that performance on the raisin detection test was impaired by ablation of the lateral striate cortex, but not by total removal of the inferotemporal visual area.

**Standard pattern discrimination.** Preoperatively, the monkeys learned the standard pattern discrimination with an average score of 128 trials and 62 errors. The scores were representative of those obtained from a total of 45 monkeys in our laboratory. The monkeys in the UNOP group (UNOP monkeys) retained the previously learned habit perfectly after a rest period of about 3 weeks. The LS group also retained the habit extremely well, scoring an average of only 3 trials and 1 error (p>0.20, U-test). The TIT group, however, required a large number of trials to relearn, the average score being 1,543 trials and 576 errors (p<0.05, U-test). Monkey 14 showed a long-lasting positional response in approximately 2,000 trials, which may account for its particularly high relearning score. In contrast to the findings on the raisin detection test, then, it may be concluded that pattern discrimination was impaired by removal of the inferotemporal cortex and not by ablation of the foveal and macular representation areas in the striate cortex.

After relearning, all the subjects were tested for retention of the discrimination following a rest period of more than 3 weeks. All retained the relearned habit perfectly (Table 1).

**Discrimination of patterns of reduced sizes.** Prior to threshold determination of the pattern discrimination, the subject was tested with the standard pair of patterns. Figure 3 indicates the scores obtained on this standard pair in each subject. They are plotted against days after the first trial of test. All monkeys attained the criterion within the first test block without any additional retraining trials. The average performance levels for the TIT, LS and UNOP groups were 97, 98 and 99\%, respectively. Thus, during the limen testing the performance levels of these three groups in the standard pattern discrimination did not differ.

The visual discrimination limens for patterns of reduced sizes are indicated in the right-hand columns of Table 1. It may be seen that from the start of the testing run, all UNOP monkeys could discriminate at least the second smallest pair (2/8). In the first run, two of them failed to discriminate the smallest pair (0.8/8), but they succeeded in the very next run and maintained this ability through-
Table 1. Scores on raisin detection, pattern discrimination and discrimination limen in Experiment I.

<table>
<thead>
<tr>
<th>Groups and subjects</th>
<th>Raisin detection</th>
<th>Standard pattern discrimination</th>
<th>Discrimination limens for reduced patterns</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>T</td>
<td>E</td>
<td>T</td>
</tr>
<tr>
<td>TIT</td>
<td>14</td>
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<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>54</td>
<td>0</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>LS</td>
<td>62</td>
<td>0</td>
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</tr>
<tr>
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<td>0</td>
<td>0</td>
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</tr>
<tr>
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<td>0</td>
</tr>
<tr>
<td>46</td>
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<td>0</td>
</tr>
</tbody>
</table>

T, trials; E, errors; Preop., preoperative; Postop., postoperative. For discrimination limens, only numerators are indicated and a common denominator of 8 is abbreviated.
Fig. 3. Scores for discrimination of standard patterns plotted against days after the first run. The scores were obtained prior to each run of determination of the discrimination limen. Numbers attached to the abscissa indicate subjects tested at respective days. TIT group: filled circles (Monkey 14), filled triangles (Monkey 45) and filled squares (Monkey 54). LS group: dots within circles (Monkey 62), crosses (Monkey 63) and asterisks (Monkey 70). Normal monkeys: open circles (Monkey 39), open triangles (Monkey 44) and open squares (Monkey 46).

out the remaining tests. Thus, their median score on the repeated determinations was 0.8/8. The LS group obtained a median score of 2/8, ranging from 5/8 to 0.8/8, whereas the TIT group obtained a median score of 5/8, ranging from 6/8 to 2/8. All the group differences were statistically significant, the TIT group differing significantly from both LS and UNOP groups ($p<0.05$, U-test on median scores) and the LS group differing significantly from the UNOP group ($p<0.05$, U-test). The TIT monkeys were given the limen test 5 or 6 times over a 2-year period. Initially they were able to discriminate only the largest test pair (6/8), but they discriminated patterns of slightly reduced sizes on the last testing run, indicating that the discrimination ability for patterns of reduced sizes was slightly but significantly improved as the training was advanced ($p<0.05$, U-test on scores of the first and last runs).

EXPERIMENT II

Experiment I established that the discrimination for patterns of reduced sizes is more severely impaired in the TIT group than in the LS group, whereas the ability of raisin detection is significantly impaired in the LS group but remains intact in the TIT group (Fig. 4). These findings are difficult to interpret inasmuch as the two tests used in Experiment I are considered to concern visual acuity. The major problem of interpretation concerns the results obtained with the TIT group, since the LS group showed moderate deficits in both kinds of acuity measure, in keeping with the results of many other studies on the effects of lateral striate lesions (WEISKRANTZ and COWEY, 1963; COWEY and WEISKRANTZ, 1967; and also see reviews by MISHKIN, 1966; GROSS, 1973; WEISKRANTZ, 1974). In the case of inferotemporal lesions, however, clear-cut sensory losses have not been
reported before. The present results, which were obtained from the two acuity tests, appeared to be contradictory. Two questions might therefore be raised. The first concerns the reliability of the discrimination limen deficit. Although the finding was repeatedly confirmed, each value of the discrimination limen was determined on the basis of a limited number of testing trials as small as 30. It could be possible that the TIT monkeys would have performed at the same level as the UNOP monkeys, if they had received more trials in each run. The second question concerns the validity of the discrimination limen test as a measure of visual acuity.

The second experiment attempted to answer both of the questions above. For this purpose, with the limit of training extended up to 1,200 trials, all the animals were trained to discriminate pluses and outlined squares which were of the same size as the standard pair in the first experiment but mounted on enlarged disc backgrounds. We will refer to this discrimination task as the variant pattern task, in distinction from the standard pattern task of Experiment I.

Methods

Subjects and apparatus. All the subjects were the same as in Experiment I and the apparatus also were the same.

Discrimination tasks. The animals were tested with two tasks, a color discrimi-
ination and a pattern discrimination. In the color discrimination red and blue paper squares, each 5.0 cm in side length and pasted on a dark-gray cardboard disc 17.0 cm in diameter, were used. The size of the colored square was the same as that of the white square used as the standard negative stimulus in Experiment I. The pattern discrimination was made using pluses and outlined squares which were the same in size as the standard patterns of Experiment I, except that these were pasted on cardboard discs which were the same size as those used in the color discrimination (see bottom of Fig. 5 where stimuli used in Experiment II are illustrated). The ratio of size between the pattern and the background was equal to that in the pair 4/8 used in Experiment I. This ratio was chosen because it was the largest ratio in the first experiment that the TIT monkeys had often failed to discriminate. In fact, the average correct performance levels of the TIT group for the pairs 8/8 (or standard), 6/8 and 4/8, across all testing sessions in Experiment I, were 97, 82 and 67 %, respectively.

Testing procedures. The testing procedures were the same as those employed for the standard pattern discrimination in Experiment I. In the color discrimination, the red stimulus was positive, and the blue, negative. The subjects were trained with raisin rewards to reach a criterion of 27 correct choices in 3 consecutive blocks of 10 trials each. In the pattern discrimination, again, the plus sign was positive and the outlined square, negative. The animals were trained to reach a criterion of 90 correct responses in 10 consecutive blocks of 10 trials each. In each discrimination 30 trials were carried out a day by the simultaneous noncorrection method. In the pattern discrimination, the animals were first tested with the standard pattern task and then with the variant pattern task. This test sequence was repeated twice, with training for the variant task being discontinued after 600
Table 2. Scores in color, standard pattern and variant pattern tasks in Experiment II.

<table>
<thead>
<tr>
<th>Groups</th>
<th>Subjects</th>
<th>Tasks</th>
<th>Colors (red vs. blue)</th>
<th>Standard patterns</th>
<th>Variant patterns</th>
<th>Standard patterns</th>
<th>Variant patterns</th>
<th>Standard patterns</th>
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</thead>
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<tr>
<td></td>
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<td>600 (F) 214</td>
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<tr>
<td></td>
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T, trials; E, errors; (F), failure in learning within training limit of 600 trials.
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trials at each stage, i.e., after 1,200 trials in total.

Results

Color discrimination. Although all the monkeys experienced the color discrimination for the first time, they learned this task quickly (see Table 2). Among the three groups, the TIT group showed the worst mean score (200 trials and 73 errors) and the UNOP group, the best one (47 trials and 16 errors), but the difference between these two groups was not significant ($p>0.05$, U-test).

Pattern discrimination. The results are shown in Table 2 and Fig. 5. All the subjects performed the standard pattern task immediately, indicating perfect retention. In the variant pattern task, all the UNOP monkeys again attained the criterion within the first 100 trials, indicating perfect transfer from the standard to the variant task. Two out of the three LS monkeys also showed a perfect transfer, though the third (Monkey 70) required 460 trials and 93 errors to learn. On the other hand, all the TIT monkeys failed to perform the variant pattern task (Fig. 5). Monkey 45, whose discrimination limen found in Experiment I had been slightly lower than the others', obtained a score of 83% in the last 100 trials, and so was close to learning; but the two others maintained a chance level of performance (56% in Monkey 14 and 61% in Monkey 54). This failure of the TIT monkeys even after 1,200 trials was unexpected, since nearly all the animals in the other groups showed a perfect transfer. The results imply that for the TIT monkeys the variant pattern task was qualitatively different from the standard pattern task and thus they had to learn this variant task as a new discrimination.

DISCUSSION

The main finding in the first experiment was that the TIT monkeys had markedly increased discrimination limens for patterns of reduced sizes but showed no impairment in the raisin detection test. The main finding in the second experiment was that, even after the TIT monkeys had relearned the standard pattern discrimination perfectly, they could not learn the variant pattern task in which the same pattern as in the standard pattern discrimination was presented on an enlarged background.

The discrimination limen in the TIT monkeys was significantly higher than in the LS monkeys, and it remained high through repeated testing runs over a 2-year period. Although the limen seems to have shown some decrement through this period, it is surprising that the discrimination ability of the TIT monkeys for patterns of reduced sizes improved so little, since during every interval between the repeated threshold determinations, the monkeys were trained on several other visual discrimination tasks and were therefore highly sophisticated (HARLOW, 1949). It is also surprising that the discrimination failures of the TIT monkeys occurred for the pair 4/8 in which patterns were reduced in size to half the standard, since this reduced size still subtended approximately 5° in visual angle. An im-
An important clue for understanding the elevated discrimination limen for patterns of reduced sizes in the TIT monkeys was obtained in the second experiment, where they were found unable to discriminate the patterns with the standard size displayed on enlarged discs, even though the size of the pattern subtended a visual angle of about 10°.

As to the nature of the underlying elevated discrimination limen of the TIT monkeys, several possible explanations may be proposed. The first possibility is that the inferotemporal visual area plays an important role in the visual acuity mechanism, as Pasik and his colleagues (Pasik et al., 1960; Valciukas and Pasik, 1965) have suggested. That is, the marked increment in the discrimination limen found in the present study may be interpreted simply as due to a loss of visual acuity. In previous studies, inferotemporal lesions were confined mainly to the anterior half of the visual area as defined by Iwai and Mishkin (1969). Thus, the possibility exists that an underlying loss of visual acuity went undetected in most earlier studies because of the use of less effective or partial lesions. In the present study, however, even the TIT lesion did not produce impairment on the raisin detection test, which is known to be sensitive to the status of visual acuity of the animal (Keating and Horel, 1972; and LS group in the present study). In Experiment II, all the TIT monkeys failed to learn the variant pattern task even after 1,200 training trials, although the size of patterns to be discriminated was as large as about 10° in visual angle. Nevertheless, they seemed to behave normally in their daily life as if they were unoperated, and no visual disorder was detectable from their behavior by simple observation. The proposal that the inferotemporal cortex is primarily involved in visual sensory function, therefore, seems unlikely, as has been concluded by the majority of investigators (Weiskrantz and Cowey, 1963; Cowey and Weiskrantz, 1967).

A second possibility is that the elevation of discrimination limen for patterns of reduced sizes reflects a difficulty in sampling pattern cues that are remote from the response site (Butter and Gekoski, 1966), perhaps as a result of an impairment of selective attention (Gross, 1973; Blake et al., 1977). When monkeys are tested in a Wisconsin General Testing Apparatus as in the present study, in general, they touch the lower part or bottom edge of the plaque (response site) to displace the stimulus card and to get bait (reward) from the foodwell. In the present test for determining the discrimination limen, the patterns of standard and reduced sizes were presented in the middle of the square background. Thus, as the patterns became smaller, there was a greater separation between pattern-cue and response site. If the TIT monkeys had difficulty in attending to pattern-cues remote from the response site, the increasing separation of pattern-cues from the response site could have resulted in a decrement of the correct performance level. A closer analysis, however, renders this explanation implausible. The distance between the bottom of the plus sign and the bottom edge of the background square was 13 mm in pair 6/8 and 21 mm in pair 4/8. The TIT monkeys often failed to
discriminate the pair 4/8, while they usually succeeded in discriminating the pair 6/8. Given the size of the monkey's fingers, it is doubtful whether this difference of 8 mm would be critical to the success or failure of attention to the pattern-cue in the TIT monkeys. In fact, as shown in Experiment II, they readily discriminated the colored squares in spite of the 50–60 mm separation between the bottom edge of the colored square and the bottom edge of the background disc. Furthermore, IWAI et al. (1976) found that, after monkeys with the same total inferotemporal lesion as in the present study had succeeded in discriminating an outlined triangle from an outlined circle placed on the same square background cards as those used in the present experiment, they failed to perform the discrimination when the positive stimulus card was simply rotated clockwise or counterclockwise by 120°. Under this condition, in which the shape of the positive pattern stimulus remained the same and only the background changed from the standard square to a rhomboid shape, the distance between the positive pattern-cue and the response site was essentially the same as before.

There is still a third possibility based on the proposal of WEISKRANTZ (1974) and DEAN (1976) that the inferotemporal cortex is involved in stimulus categorization; the marked elevation of discrimination limen in the TIT monkeys may reflect a difficulty in categorizing all the differently sized patterns as the same. As shown in Experiment II, however, as well as in the study by Iwai et al. referred to above, the TIT monkeys failed to learn the discrimination between a pair of stimulus cards that carried exactly the same patterns of the same sizes as in the standard pair. Also, the elevation of the discrimination limen for patterns of reduced sizes in the TIT group may scarcely be explained in terms of disorder of memory, because in the limen test in Experiment I they could discriminate if test pairs were somewhat larger and in Experiment II they could perform the color discrimination as well as the UNOP monkeys.

The final proposal, which appears to be the most reasonable at present, is based on the view that the inferotemporal cortex is intimately concerned with pattern perception (IWAI and MISHKIN, 1968). The findings from both Experiment II and the study by IWAI et al. (1976) suggest that, when the TIT monkeys finally learned to discriminate the standard pattern task, they did not do so on the basis of normal pattern perception. Rather, they must have utilized some perceptually simpler but less salient cue other than the salient pattern-cue (BUTTER and GEKOSKI, 1966), although from the present results we cannot identify it. Nevertheless, since they learned the color discrimination easily, and since after extended training they relearned the standard pattern discrimination but still failed to learn the variant pattern task, it is reasonable to assume that they treat pattern discrimination as though it were a hidden-feature detection task in which salient patterns are not discrimination cues. Consequently, as the size of the pattern was reduced, or, conversely, as the size of the background was enlarged, the cue that the monkeys had discovered in the standard discrimination may have become less clear and then
disappeared. In fact, they behaved as though they were being trained on an entirely new task although the monkeys in the other groups showed a nearly perfect transfer.

Initially, the discrimination limen test for patterns of reduced sizes was introduced to examine visual acuity. Ordinarily, if the pattern perception mechanism is intact, the discrimination limen for patterns of reduced sizes may be a valid and sensitive measure of acuity status, as may have been the case with both LS and UNOP groups. According to the present interpretation, however, this test is not appropriate for measuring visual acuity function in the TIT monkeys, since their pattern perception is not intact.

The nature of the impairment following inferotemporal lesions is still highly controversial. In this paper, a certain behavioral deficit has been interpreted in terms of a disturbance of pattern perception. However, this does not imply that the inferotemporal cortex is involved only in the mechanism of pattern perception. Rather, we assume that the inferotemporal cortex is involved in many processes of high-level visual function. IWAI and MISHKIN (1968) and COWEY and GROSS (1970) have demonstrated that the function of the inferotemporal cortex is not a unitary one; the anterior subdivision of the inferotemporal visual area (area TE) is closely concerned with visual memory or visual association, while the posterior subdivision (area PH or TEO) is involved instead in visual perception or selective attention. The present findings, therefore, may reflect mainly damage to the neural mechanism served by the posterior inferotemporal cortex, though the total inferotemporal visual area was removed.

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