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Lesions

The general surgical and histological procedures that were used have been described previously (Mishkin, 1954). The lesions were bilateral and were made in one stage. The inferotemporal lesions included the middle, inferior, and fusiform gyri, sparing the polar cortex anteriorly and ending posteriorly about $\frac{1}{2}$ cm. in front of and parallel to the ascending inferior occipital sulcus. One S sustained a slight amount of damage to the left superior temporal gyrus. With this exception, the area of damage corresponded closely to von Bonin and Bailey's (1947) Areas TE and TF. Removing this area resulted in a small amount of retrograde degeneration in *n. pulvinaris medialis*.

The occipital lesions included the polar tip and extended over the lateral surface from the longitudinal fissure down to the inferior occipital sulcus and forward to the lunate sulcus. A small strip of prestriate cortex posterior to the lunate sulcus was thus included in the lesions. An area was not removed during surgery but degenerated postoperatively, probably as a result of disruption of its pial blood supply. The total area of damage corresponded to von Bonin and Bailey's (1947) Areas OC and OB on the lateral occipital surface. According to Talbot and Marshall (1941), each lateral occipital surface receives projections from about nine degrees of the central visual field. Removing this area caused retrograde degeneration in the intermediate wedge-shaped third of the lateral geniculate bodies and questionable degeneration in posterior areas of *n. pulvinaris inferior* contiguous to the lateral geniculates. Reconstructions of the lesions and representative cross sections of the cerebral hemispheres and thalami are presented in Figure 1.

Procedure

Apparatus and Tests

The Ss were trained in a Wisconsin General Testing Apparatus, placed within an air-conditioned, soundproofed room. A series of eight tasks was presented to each S. Four of the tasks—Visual Fields and Acuity, two Patterned-String tasks, and Size-Discrimination Thresholds—were included as potential measures of sensory defects. The four others—Food Recognition, Object Learning Set, Pattern Discrimination Learning, and Discrimination Transfer—were included as potential measures of impairment in learning. The eight tasks are described below in the order in which they were given.

Visual Fields and Acuity. A plywood panel, painted flat black, was placed on the floor of the testing compartment. The S was trained to pull in a coarse white string placed on the black panel to obtain a peanut attached to the far end of the string. Black surgical thread of four sizes was substituted in formal testing (USP 6–0, 0.08 mm. in diameter; USP 5–0, 0.15 mm.; USP 0, 0.3 mm.; and USP 3, 0.6 mm.). One end of the thread was 3 in. from S's cage, either in the center or 4 in. to the right or left of center. The end with the peanut attached was always in the center, 15 in. from the cage; to permit recovery of the thread after a response, it actually extended beyond this far "end,"

through a hole in the plywood panel. A schedule was followed which balanced the order of trials with respect to size of thread and side of presentation. Latency of response and unusual or incorrect responses were noted. Twenty-four trials (two trials for each size-side combination) were given 3 days and 1 day before operation. Twelve trials were given 1, 4, and 7 days after operation.

In a second test of visual fields, ten peanuts were placed upon the floor of the testing compartment to form a line parallel to, and 3 in. from, the front of the cage. The order of choice and the time required to respond were recorded. This test was given one day before operation and four and seven days after operation.

Food Recognition. Ten objects were placed in a row on the compartment floor. Included were food and nonfood objects, such as pieces of soap, erasers, screws, etc. The nature and latency of responses were noted. This test was presented on the same days as the second visual-fields test described above.

Patterned Strings: Random Presentation. The floor of the testing compartment was covered with a black panel, and pairs of linked chains were used for "strings." The ends of the chains near S were 6 in. from the cage and 6 in. apart; the other ends were 21 in. from the cage and either 6 in. or 1$\frac{1}{2}$ in. apart. A peanut was attached to the far end of one of the chains. As in the Visual Fields and Acuity test, each chain extended beyond its visible far "end" through a hole in the panel. The designs of the eight problems are represented in Figure 2.

Each of the 16 possible presentations was given once a day for 15 days, the order of presentation varying daily. A response was scored when the animal touched either chain. Except as noted, noncorrection procedure was used in this and all the tasks described below. These tasks were all given after operation only. The training period extended from about two weeks to one year postoperatively.

Patterned Strings: Criterional Training. The Ss were trained on the "single-crossing" problem (Fig. 2, No. 5) for 30 trials a day to a criterion of 90% correct in 30 trials. Gellermann's (1933) sequences were used on this and subsequent tasks to determine the order of left-right placement of the reward. After completing this problem, Ss were trained on the "single-crossing with bend" problem (No. 7) and finally on the "double-crossing" problem (No. 8). Because of the long response latencies of some Ss on some problems, a trial was ended and scored as an error if no response was made within 1 min. Training on a task was stopped at 500 trials if an S had not reached criterion.

Pattern-Discrimination Learning. In this and the following tasks a $\frac{3}{4}$-in. board with two foodwells 1$\frac{1}{4}$ in. in diameter and 15 in. apart, was placed on the floor of the test compartment. A peanut was placed in one well and covered by the "positive" stimulus of a given pair; the empty well was covered by the "negative" stimulus. The discriminanda for this task were discs of $\frac{1}{4}$-in. masonite, 3 in. n diameter. The figures were applied with flat-black paint on flat-white backgrounds (or the reverse) and were designed to cover half the surface area of the discs.
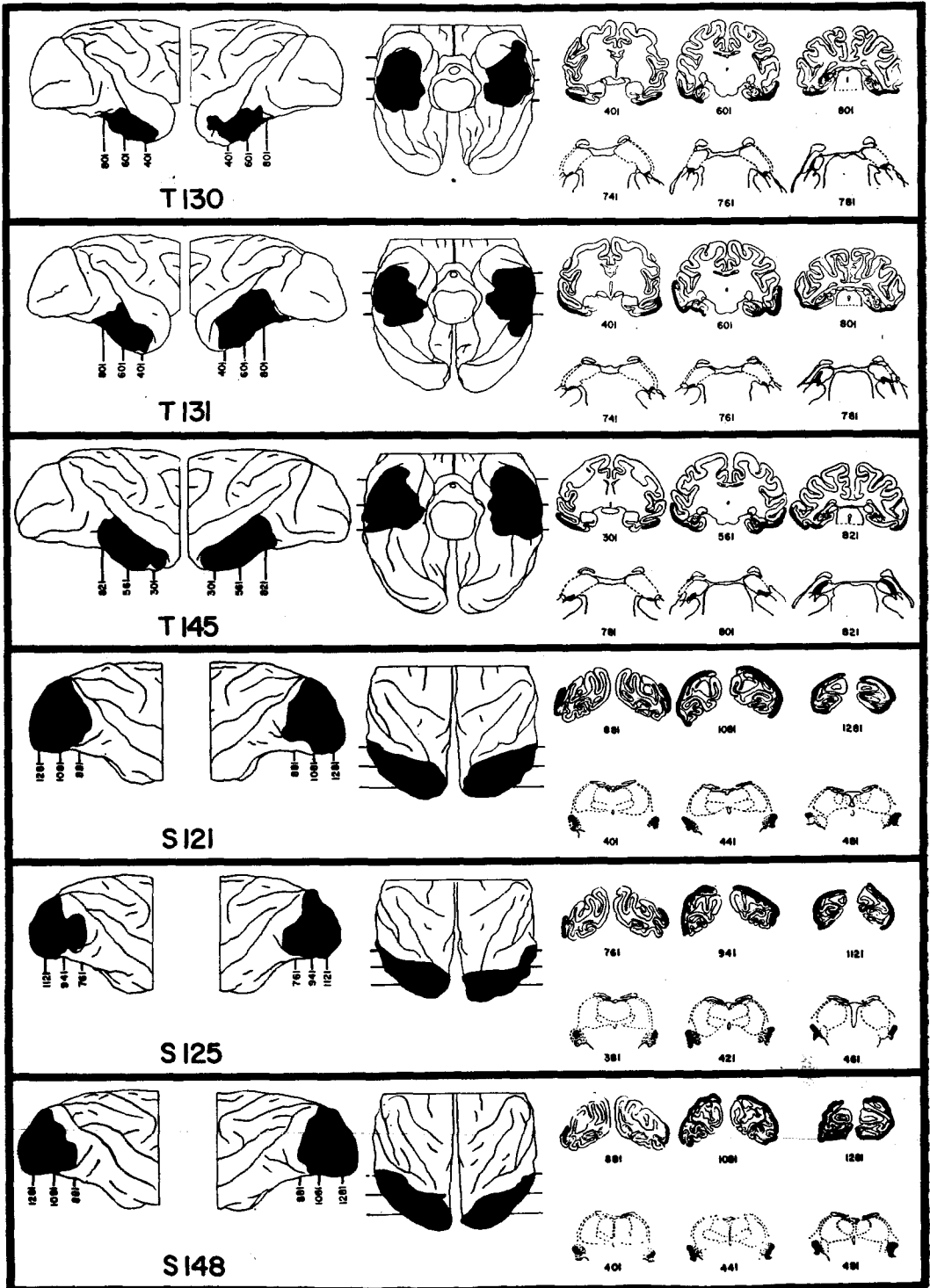
FIG. 1. Reconstructions of the lesions and representative cross sections of cerebral hemispheres and thalami.

Thirty trials were given daily on a given pair of stimuli until S met the criterion of 90% correct in 30 trials. On the first problem only, Ss were stopped at 500 trials if they had not reached criterion. The five discriminations were given in the order indicated in Table 1.

Object Learning Set. The discriminanda for this task were three-dimensional colored objects. Forty-eight pairs of objects were chosen randomly from a larger group. Each day one pair was presented to a criterion of 9 consecutive correct trials. In the rare case in which criterion was not reached in 40 trials, training was completed in a second session on the same day.

Size-Discrimination Thresholds. The discriminanda were circular discs of thin masonite. All were painted flat black and differed only in diameter.

The Ss were first trained for 30 trials a day to choose a 3-in. disc paired with a 6-in. disc to a criterion of 25 consecutive correct choices. The Ss were then given 50 trials (25 trials a day for two days) in which the positive 3-in. disc was paired with a negative 5-in. disc. In turn, discs of 4, 3½, 3¼, 3⅛, 3 1/16, and, finally, 3 in. were used as the negative stimulus for 50 trials each. All discs were repainted frequently.

Discrimination Transfer. Two pairs of discriminanda were used: (a) masonite discs, 3 in. in diameter, one covered with green (positive), the other with red paper; (b) 4-in. cardboard squares each with alternating black and white paper stripes, one oriented so as to present vertical striations (positive), and the other horizontal striations.

Each pair was first presented as a simultaneous discrimination following the same procedure as that used for the Pattern Discriminations. After reaching the criterion on a given pair, S was trained to the same criterion on a "go, no-go" successive discrimination presented on a testing board with a single centered foodwell. The correct responses in this situation were to displace the single stimulus if it had been previously positive and to refrain from displacing it if it had been negative. The Ss were permitted 5 sec. in which to respond. Correct "no-go" trials were not rewarded; incorrect "no-go" trials were simply continued for the full 5 sec. in the green-red discrimination, and were corrected by the rerun method in the vertical-horizontal discrimination.

Statistical Procedures

On each of the four "sensory" tasks Whitney's (1951) three-sample test was used to evaluate the hypothesis that the striate group was inferior to the two other groups. If a significant difference ($p < .05$) was obtained, the Mann-Whitney test (1947) was then used to determine whether the inferotemporal group was inferior to the unoperated controls. The same statistical procedures were used on each of the four "learning" tasks to determine whether the inferotemporal group was inferior to the two other groups, and, if so, whether the striate group was inferior to the unoperated controls. Except as noted, the total error scores for each S on all the subtests in a given task were used to evaluate the hypotheses.

Four out of the eight tasks failed to distinguish between the effects of inferotemporal and lateral occipital lesions, although differences between operated and normal Ss were sometimes noted. The results on these four, two sensory tasks and two learning tasks, are described first.

Visual Fields and Acuity. On the day after operation, all Ss looked well and presented no obvious signs of motor loss or incoordination, although the three Ss with striate lesions "past-pointed" when food was handed to them. On this first day most of the operated Ss failed to pull in the threads on some of the trials, but by the fourth day all Ss responded quickly and consistently.

Comparing preoperative performance with performance on the fourth and seventh postoperative days, two striate and two inferotemporal Ss showed small increases in latency. Despite this, they responded as quickly as the slowest unoperated S. The increased latencies were not restricted to threads of smallest diameter, nor to threads in a particular position. Furthermore, in the second visual-fields test, none of the Ss consistently neglected peanuts in a particular place on the board.

Patterned Strings: Random Presentation. Although this task did not differentiate the striate group from *both* of the other groups, it is of interest that each of the three striate Ss accumulated more total errors than the poorest unoperated control. The data suggest that this over-all difference between the striate and control groups is accounted for mainly by the problems of intermediate difficulty (Fig. 2, No. 3, 4, and 5).

Food Recognition. No abnormalities were detected in any animal. None repeatedly examined or approached nonfood objects.

Discrimination Transfer. Inferotemporal Ss were expected to have greater difficulty than the other Ss in learning the successive problems after learning the corresponding simultaneous discriminations. This result was obtained on the discrimination between vertical and horizontal striations, but was nullified by the results for the color discrimination on which the striate group performed most poorly. It is of interest that the group which performed
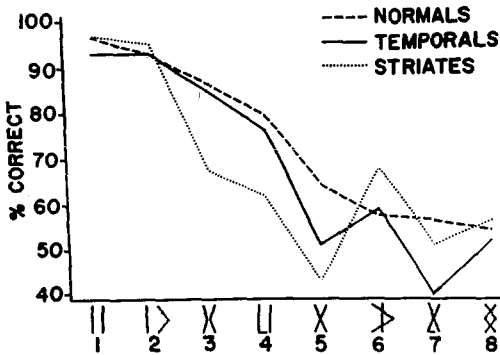
FIG. 2. Mean performance of the three groups on Patterned Strings: Random Presentation. Problems are shown in the order of their difficulty for the normal group.
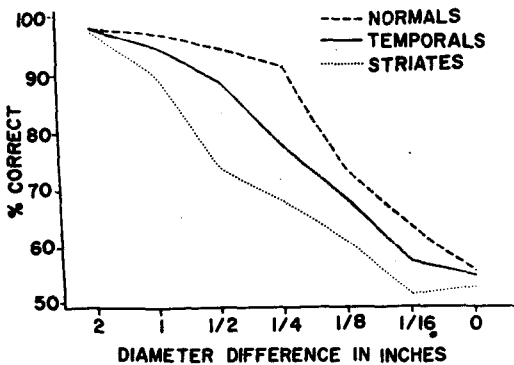

FIG. 3. Mean performance of the three groups on Size-Discrimination Thresholds.

most poorly on a given pair of stimuli when these were presented successively, required the longest time to discriminate them initially.

In contrast with the four tasks just described, each of the four others differentiated between the operated groups. On two of these four tasks, however, both operated groups were inferior to the unoperated controls. The results on these two, one sensory task and one learning task, are described next.

Size-Discrimination Thresholds. All *S*s quickly learned the initial discrimination between the 3-in. and the 6-in. discs. The mean error scores were 5.3 for the inferotemporal group, 3.3 for the striate group, and 3.7 for the control group. The data gathered on subsequent threshold testing are graphed in Figure 3. The striate group performed most poorly, but the inferotemporal *S*s were also impaired relative to the controls. The same results are obtained considering either the

over-all error scores or difference limens (the latter computed as the interpolated size difference which an *S* discriminated 75% of the time).

Pattern-Discrimination Learning. Mean error scores for Pattern-Discrimination Learning are given in Table 1. On the first discrimination none of the operated *S*s met the criterion within 500 trials. On subsequent discriminations the inferotemporal *S*s learned most slowly, but the striate group was also retarded in learning as compared with the controls.

The degree of deficit for the operated *S*s was roughly proportional to the difficulty of the discriminations as measured by the error scores of the normal group. For all three groups the later problems were learned more quickly than the earlier ones, but whether this order of difficulty was related to order of presentation or to differences inherent to the discriminations cannot be determined from these data.

While the two tasks just described differentiated between the inferotemporal and striate groups, better differentiation was found on the two tasks described next. The results on these indicate impairment in one operated group but not in the other.

Patterned Strings: Criterional Training. Mean error scores on the three patterned-string problems presented to criterion are given in Table 2. Only in the striate group did any *S* fail to meet the criterion; in this group there were five failures out of a possible nine.

The *S*s often adopted extreme position habits, and while maintaining these, frequently

TABLE 1

Pattern-Discrimination Learning

(Mean errors to criterion)

Problem	Normal Controls	Inferotem-porals	Lateral Striates
Cross–diamond	131.3	244.3[a]	244.7[a]
Thin–wide stripes	32.0	209.7	127.0
Square–checks	75.7	196.0	153.7
Star–circle	12.3	187.0	116.7
Upright–inverted triangle	29.3	183.0	98.0
Total	280.6	1020.0	740.0

[a] Testing discontinued—no *S* had reached criterion within 500 trials.

TABLE 2
Patterned Strings: Criterional Training
(Mean errors to criterion)

Problem	Normal Controls	Inferotem- porals	Lateral Striates
Single crossing	3.7	7.3	61.3
Single crossing with bend	3.3	44.0	148.0[a]
Double crossing	102.3	164.7	292.3[a]
Total	109.3	216.0	501.6

[a] Includes Ss that had not reached criterion and were stopped at 500 trials.
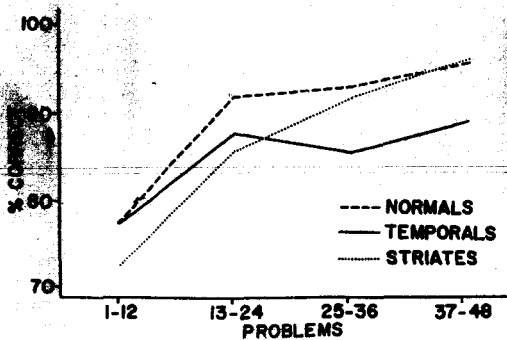

FIG. 4. Mean performance of the three groups on Object Learning Sets. Points are based on performance on Trials 2 to 9 for the four blocks of problems indicated.

developed large latency differences: correct responses were performed more quickly than incorrect responses, and on occasion, there was no response at all. This striking behavior was noted among all groups, but in the inferotemporal and control groups the Ss eventually abandoned their position habits and went on to meet the criterion. No significant difference was found between the two latter groups.

Object Learning Set. Interproblem learning curves for the three groups are presented in Figure 4. The curves are based on Trials 2 to 9 for each of the 48 problems, divided into four successive blocks of 12 problems each; the scores for the last block of problems were used in testing for differences in learning-set formation.

Despite their marked deficit relative to the other two groups, the inferotemporal Ss showed some evidence of improvement in learning during the initial stages of training. The striate group appeared to perform poorly at first, but reached a final level of performance equal to that of the control group. No significant difference was obtained between the scores of these two groups, and inspection of their curves suggests that in neither case had the limits of learning-set formation been reached.

DISCUSSION

Direct comparison between the effects of lateral occipital and inferotemporal lesions has revealed many impressive similarities, but also some major differences.

The most striking differences were obtained in the patterned-string task, on which only the striate group was impaired, and in the learning-set problem, on which only the inferotemporal group showed persistent impairment. Two different types of deficit must be hypothesized to account for these findings, and it seems reasonable as a first approximation to label them "sensory" and "learning" deficits.

Although a clear-cut separation between these two types of impairment was found on the patterned-string and learning-set problems, it cannot be claimed that striate lesions produce *no* impairment in learning, or, conversely, that inferotemporal lesions produce *no* sensory defects. In learning to discriminate painted patterns, for example, the animals with striate damage exhibited significant retardation relative to normals. This deficit, of course, might be attributable to sensory defects, which could have interfered with the discrimination of small differences between the painted patterns. (It might be speculated, also, that their relatively poor performance on the color discrimination in the discrimination-transfer task, and on the object discriminations in the initial stages of the learning-set task, resulted from a specific deficit in color vision following bilateral removal of the macular projection field.) For the present, however, the notion that striate lesions produce sensory defects exclusively must remain in doubt.

The analogous attempt to restrict the effects of inferotemporal lesions to impairment in learning meets with similar difficulties. Pulling in small surgical threads is clearly inadequate as a measure of visual acuity, since striate damage which caused severe degeneration in the macular portions of the lateral geniculate

bodies had no consistent effects on performance in this task. It is not surprising, therefore, that inferotemporal damage was also without consistent effect. If, however, the size-discrimination threshold is accepted as a valid measure of acuity, then it must be concluded that inferotemporal lesions do produce a loss in visual acuity, although less than lateral striate lesions do.

The demonstration that there are both similarities and differences between the effects of lesions in the two "visual areas" supports an intermediate position (Hebb, 1949) between the two extremes of older theory. One extreme has set up a sharp dichotomy between "receptive" and "integrative" visual functions, with the suggestion that these are served by "primary" and "associative" cortical areas, respectively (Lange, 1936; Nielsen, 1946). The other proposed that there is *no* separate localization for "receptive" and "integrative" functions (Bender & Teuber, 1949; Lashley, 1948). The compromise indicated by the present experiment is that each of the two areas studied serves both visual functions, but not equally well. The results suggest a neural model in which the centrally located inferotemporal area is related, perhaps via the striate cortex, to the periphery, and hence, to the neural mechanisms of acuity. However, the inferotemporal area adds a new neural dimension in vision (emerging perhaps as an elaboration of the acuity mechanisms) which serves more complex discrimination functions related to learning.

SUMMARY

Three monkeys with lateral striate lesions, three with inferotemporal lesions, and three unoperated controls were trained on a series of eight visual tasks. Four of the tasks differentiated between the operated groups, the differences being in the opposite directions for two pairs of tests. The striate group was inferior to the others on patterned-string problems and on size-discrimination threshold, while the inferotemporal group was inferior to the other two groups on painted-pattern discriminations and on object learning set. The dissociation between the effects of striate and inferotemporal lesions was not complete, however. The striate group showed some impairment on the painted-pattern discriminations, and the inferotemporal group showed some impairment on the size-discrimination threshold. The results favor a theory which views the two "visual areas" as interdependent but which grants priorty in acuity functions to the striate cortex while emphasizing the importance of the inferotemporal cortex for visual functions related to learning.

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COMPARISON OF THE EFFECTS OF INFEROTEMPORAL AND LATERAL OCCIPITAL LESIONS ON VISUALLY GUIDED BEHAVIOR IN MONKEYS[1]

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Evidence has accumulated indicating that there are *two* "visual areas" in the posterior cerebral cortex of monkey: the striate cortex of the occipital lobe and the neocortex in the inferotemporal region. Damage to either one may produce impairment in visually guided behavior, leaving behavior controlled by other senses relatively intact (Orbach, 1955; Pribram & Barry, 1956; Weiskrantz & Mishkin, 1958; Wilson, 1957). The effects of the two lesions have never been compared directly, but indirect comparison suggests that within the visual modality the two deficits are distinctly different from each other. Thus, inferotemporal lesions impair learning, retention, and transfer on a wide variety of visual discrimination problems (Chow: 1951, 1954; Pribram & Mishkin, 1955; Riopelle, Alper, Strong, & Ades, 1953) without affecting performance on various sensory tests, i.e., tests designed to measure extent of visual fields (Riopelle et al., 1953) and visual acuity (Chow, 1951; Mishkin, 1954). Large, subtotal occipital lesions, on the other hand, produce the deficits from which scotomata (Harlow, 1939; Settlage, 1939) and reduced acuity (Spence & Fulton, 1936) have been inferred, without greatly affecting performance on visual discrimination problems (Klüver, 1937; Settlage, 1939).

On closer examination, however, the apparent contrast between these two types of visual impairment begins to fade. It was found recently, for example, that after monkeys with inferotemporal lesions are trained to discriminate visually a large difference in size they may still show impairment in discrimination if the size difference is reduced (Mishkin & Hall, 1955). It is difficult to reconcile this finding of increased difference limens with the notion that inferotemporal lesions produce impairment limited to learning. As to the supposition that partial striate damage results only in sensory defects, the evidence is incomplete. Most experiments dealing with the effects of striate damage on visual discrimination have been concerned chiefly with the final performance of the operated animals, and it is on this measure that little or no impairment has been observed. The possibility remains that subtotal striate lesions retard the *rate* of discrimination learning much as inferotemporal lesions do.

In short, the differences between the effects of inferotemporal and partial striate damage may not be nearly as great as they first appeared to be. To specify accurately the differences that do exist, and to use these differences in analyzing the roles of the two areas in visually guided behavior, the effects of damage to the two areas must be compared directly. In the following experiment monkeys with inferotemporal lesions, monkeys with lateral occipital lesions, and unoperated monkeys were compared on a series of "sensory" and "learning" tasks including those which earlier work suggested were most likely to differentiate between the two operated groups.

METHOD

Subjects

Nine experimentally naive, immature rhesus monkeys served as Ss. They were divided into three groups of three Ss each.