

VISUAL DISCRIMINATION FOLLOWING SUCCESSIVE TEMPORAL ABLATIONS IN MONKEYS

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INTRODUCTION

PERFORMANCE on a variety of visual perceptual tasks may be disturbed following injury or disease of the so-called "association areas" of the cortex in man. Thus impairment may commonly be elicited by tests of sorting and classification (Teuber, Battersby and Bender, 1951; McFie and Piercy, 1952); or when the patient is required to distinguish between "figure" and "ground" (Teuber and Weinstein, 1956); or even on the less complex tests of discrimination between dissimilar stimulus figures (Battersby, Krieger and Bender, 1955). However, location of the cortical lesion would not seem to be an important determinant of the deficit on any of these tests in man. Nor yet are such disorders of perception a regular consequence of a lesion in the association cortex.

A different conclusion concerning the necessary site of the lesion may be drawn when clinical impairment on tests of "spatial perception" is considered. Thus the disorders termed "apractognosia" (Hécaen, Penfield, Bertrand and Malmo, 1956), "amorphosynthesis" (Denny-Brown and Banker, 1954) and "visual-spatial agnosia" (Ettlinger, Warrington and Zangwill, 1957) have been generally reported to follow lesions situated in the posterior parietal areas. This same site of injury has been implicated for impairment on a quantitative test of spatial orientation in an unselected series of cases (Semmes, Weinstein, Ghent and Teuber, 1955). However, the earlier view that such disorders of spatial perception were specific to the visual modality can no longer be sustained (Ettlinger *et al.*). In fact "the parietal group showed a slightly greater percentage decrement on the tactual maps than on the visual series" (Semmes *et al.*). It would therefore appear that no consistent relationship has as yet been established in an unselected series of clinical cases

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between a disorder of perception¹ confined to the visual modality and any one site of lesion within the association cortex.

It is in part by contrast to these current clinical findings that a deficit occurring in monkeys as a consequence of bilateral temporal lobe lesions merits further consideration. For this impairment is not expected to follow the appropriate specifiable lesion virtually without exception. Moreover animals giving evidence of this visual disorder are unimpaired under comparable conditions of somato-sensory and auditory testing (Pribram and Barry, 1955; Wilson, 1957; Vignery and Mishkin, 1958; Wegener, 1959). It might also appear unusual if not paradoxical, on general principles of progressive encephalopathy of function that a behavioural deficit should be linked with a lesion of a small part of the cortex more reliably in the monkey than in man. Therefore the disorder of visual perception in monkeys with temporal lobe ablations may still perhaps at some future time be called upon rather as a paradigm for, than contrast to, the clinical observation of perceptual disruption in man.

A comparison between this "psychic blindness" in monkeys and this extraordinarily rare clinical condition, the associative mind-blindness of Lissauer, was already drawn by Klüver and Bucy in 1937. (Lissauer had traced similarities between his clinical instances and certain animal preparations of Munk.) A more detailed quantitative analysis of the behavioural changes in monkeys was presented by Blum, Pribram and Mishkin in 1950. Thereafter the more precise delineation of the smallest effective lesion and also of the behavioural consequences followed rapidly. For example the studies of Chow (1952) and Mishkin (1954) indicated that bilateral removal of the inferior temporal cortex was sufficient to reproduce the visual disorder. Moreover the behavioural, dietary and sexual changes associated with the more radical procedure of Klüver do not occur following this limited inferotemporal cortical ablation. Instead they can be correlated with damage to the anterior sectors of the temporal lobe. On the other hand a *unilateral* temporal lobectomy or cortical ablation was found to be not sufficient to produce to any appreciable visual deficit (Mishkin and Pribram, 1954).

As a rule the animals' visual perception has been assessed by the two-choice discrimination procedure in which one of two visual cues is consistently rewarded irrespective of its position. Animals with bilateral temporal excisions were then impaired whether the cues differed in hue, brightness, size or form (Mishkin and Hall, 1955). Provided that the test exceeded an intermediate level of difficulty (as judged by reference to the performance of unoperated animals on a

¹In the present context the term "perception" is held to apply neither to the optokinetic response (Carmichael, Dix and Hallpike, 1954) nor to tests of "spatial intelligence" (Milner, 1954).

tasks). This post-operative impairment became evident both during relearning of a discrimination originally acquired before surgery and during initial post-operative acquisition of a discrimination. However, the incidental field defects, following some but not all of the temporal lesions, or possible areas of amblyopia could not, it was claimed, be held responsible for this comprehensive visual perceptual disorder. For dissimilar patterns of breakdown on a variety of visual tasks resulted from a comparison between the effects of infero-temporal excisions and of striate lesions involving the cortical macula. For example the striate animals were inferior to temporal animals on a test of the difference threshold for visual size, whereas the temporal animals were inferior to the striate animals on a standard test of visual discrimination learning (Wilson and Mishkin, 1959). Nor yet can this visual disorder be attributed to any simple impairment of learning or of "immediate memory" confined to the visual modality. For temporal animals may achieve a higher standard of performance than do control animals on tests of delayed reaction in which correct choice of response depends upon learning to remember the nature of an immediately preceding cue (Pribram and Mishkin, 1956).

Bilateral infero-temporal ablations in monkeys would then seem to have as their consequence a widespread disorder of perception that is specific to the visual modality (since somato-sensory and auditory discrimination remain unimpaired). Loss of sensory capacity as a result of field defects appears neither sufficient nor necessary to give rise to the deficit. Nor yet has general learning ability or immediate memory become defective in these animals. The disturbance following temporal lesions is not therefore obviously dependent upon disruption of any one or more of the functions that would appear *a priori* to be concerned in visual discrimination by the intact animal.

Before resorting to more complex interpretations it was nevertheless thought advisable to examine what contribution *qualitative* or *relative* changes in elementary visual sensory efficiency might make to the genesis of this perceptual disorder. For it could be argued that previous studies had succeeded in excluding the aetiological significance only of relatively dense or absolute field defects. Moreover even areas of absolute blindness cannot be easily charted in the monkey, so that qualitative or relative sensory changes might readily escape detection. Also some indirect support for this point of view was thought to be forthcoming from studies of somato-sensory discrimination. Thus a disturbance in this modality has been reported to occur as a result of bilateral parietal lesions in monkeys, and has been regarded as analogous to the visual disorder following temporal excisions. When animals were tested on a variety of somato-sensory discriminations separately with each hand after *seriatim* removals of the temporo-parietal areas, the

performance with the two hands was found to differ unexpectedly (Blum *et al.*). For performance with the first hand to be tested following surgery (that is, with the post-operatively preferred hand, being on the side opposite to the first lesion) was usually superior to that achieved with the second hand to be tested (that is, with the post-operatively non-preferred hand, being on the side opposite to the second lesion). These results were obtained although the discrimination had been acquired pre-operatively with the hand giving the inferior post-operative performance. They are contrary to the expectation of improvement in performance with the second hand following prior post-operative relearning with the other. It would, in fact, almost seem as if the two hands operate independently in relearning a somato-sensory discrimination following bilateral parietal lesions.

An investigation was therefore undertaken to determine whether qualitative or relative alterations in elementary visual sensory capacity might account for the defect of visual discrimination in temporal monkeys. The assumption was made that such (modality-specific) changes would take place only in the visual half-fields opposite to a unilateral lesion. Then the previously demonstrated absence of impairment consequent upon unilateral temporal ablations would be comparable to the absence of impairment expected as a consequence of a unilateral lesion giving rise to a complete homonymous hemianopia. On the other hand at least as severe a disturbance would be expected to follow a unilateral temporal removal made on the side of the brain opposite to a lesion causing a complete homonymous hemianopia as would be expected to follow bilateral temporal removals. Again, the addition of a second temporal removal from the same side of the brain as the lesion causing the hemianopia would not be expected to give rise to further impairment. More specifically, it was predicted, firstly, that animals having a *left* unilateral temporal excision combined with a section of the *left* optic tract would remain unimpaired; secondly, that animals having a *right* unilateral temporal excision combined with a section of the *left* optic tract would be as severely impaired as animals having bilateral temporal excisions; and finally, that addition of a *left* temporal excision to pre-existing *left* tract and *right* temporal lesions would give rise to no further impairment. These predictions were put to experimental test.

METHOD

Subjects.—12 previously untrained rhesus monkeys served as subjects for this experiment. Their weights ranged from 5 to 6½ lb. at the beginning of training, and from 6 to 7½ lb. at the time of the last surgical operation upon each animal.

Operations.—Surgical procedures were undertaken at 6 different sites of the brain. However, only one lesion was made at each operation (except in the case of the first operation upon animals 11 and 12). All animals received at least two lesions serially. The lesions comprised: total section of the left, or the right optic tract; aspiration of the

left, or the right inferotemporal-preoccipital cortex; aspiration of the right anterolateral frontal cortex; and total division of the corpus callosum.

All operations were performed aseptically under intraperitoneal nembutal anesthesia. The optic tract was visualized from an anterior approach after removal of the zygoma and elevation of the temporal pole. It was then cut as far behind the chiasm as proved practicable. Silver clips were applied to the left tract behind the section in the case of animals 1 and 2. In animals 4 and 12 the right optic tract was cut three weeks and five months respectively after section of the left tract. This operation was considered essential in order to secure behavioural verification of the effectiveness of the left tract section in animals that had performed contrary to expectation on the pattern discrimination. Cortex was aspirated by means of a small-gauge sucker. The temporal removals were intended to reproduce the lesions made by Mishkin and Hall, that is, in brief, to extend ventrally and medially from the superior temporal sulcus, and reach backwards as far as the vein of Labbé and the inferior occipital sulcus. The frontal ablations were designed to extend forwards from the arcuate sulcus over the entire lateral surface. The frontal poles were amputated within an arc of about 2 cm. from their tips. Exposure of the corpus callosum required the coagulation of 3 large bridging veins to the longitudinal sinus on the left side. The callosum could then be divided along its entire length under full visual control by blunt dissection. This procedure was recognised to involve damage to the fornix and penetration into the third ventricle.

Histological procedures and findings.—Following completion of testing the animals were anaesthetized and their brains perfused with formalin, removed, examined macroscopically, and then prepared for histological study. Serial coronal sections of 50 μ thickness were cut. Every tenth section was stained with thionin, and the remaining nine discarded except in the region of the optic tract transections, where selected sections were stained by the Loyez method.

The cortical removals were found to correspond in general to the surgical intentions, those in the left hemisphere being somewhat more extensive than those in the right. Macroscopically the optic tract sections were seen to be placed at between 2 mm. and 5 mm. behind the chiasm. It was found possible to verify by histological study that the left optic tract had been completely cut in all animals and that the corpus callosum was divided along its entire length in the 3 animals receiving this lesion.

Fig. 1 shows reconstructions of the cortical lesions and selected cross sections in representative cases (animals 2, 7 and 12). From the histological sections the extent of any incidental damage to structures in the neighbourhood of the transected tracts was determined.

In most of the animals the antero-inferior part of the left temporal lobe, including the amygdaloid nucleus, was involved as a consequence of displacing the temporal pole in dividing the optic tract. However, such damage extended on to the lateral surface only in the case of animals 3, 5, 6, 9 and 11, and in no instance sufficiently far backwards to encroach upon any cortex that would properly be included in an infero-temporal removal.

Section of the left optic tract also caused incidental damage in most animals to the globus pallidus, and to some fibres of the internal capsule. Other structures in the neighbourhood of the lesion showing occasional damage were as follows: the putamen; the habenula and hypothalamus; the ansa lenticularis; the anterior commissure; the caudate; the thalamus.

In 2 of the 3 animals in which the corpus callosum was cut, there was incidental damage to the cortex. In animal 3 a large area of degeneration was found in the left frontal lobe, extending from the central sulcus to within 1 cm. of the frontal pole, and from the superior arcuate sulcus over the medial surface of the lobe. A much smaller

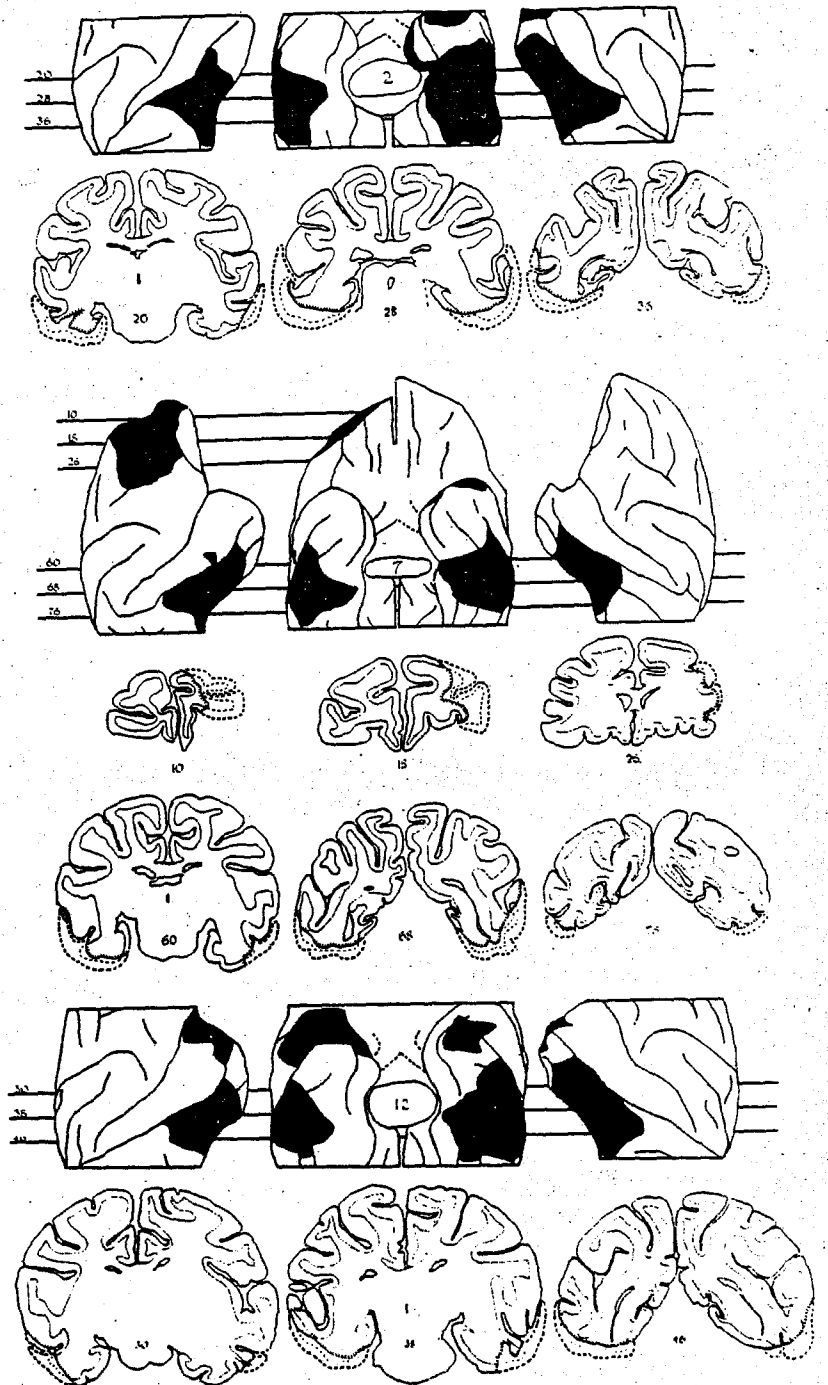


FIG. 1.—Reconstructions of cortical lesions and of areas of incidental damage in animals 2, 7 and 12, together with selected cross sections. Black indicates the extent of cortical damage in the surface views.

area of degeneration (about $\frac{3}{4}$ cm. in diameter) was seen in the left post-central parasagittal cortex of animal 6.

Apparatus.—The animals were wheeled to the testing room in a transport cage. They were able to grasp the cues from this cage by reaching through vertical bars spaced 2 in. apart. One of the 2 screens forming part of a large wooden enclosure surrounding the transport cage was always interposed between the animal and the experimenter. The forward one-way vision screen could be raised in between the transport cage and the cues to allow the experimenter to conceal the reward under either cue without the animals' knowledge. The rear one-way vision screen separated the experimenter from the cues when the forward screen was lowered. The animal could be observed at all times by means of this apparatus.

Tests.—All animals were taught to discriminate between an outline square and a cross. The outside edges of the square measured $1\frac{3}{4}$ in. and the inside edges were 1 in. long. The arms of the cross measured $1\frac{3}{4}$ in. tip to tip and were $\frac{1}{2}$ in. wide. These 2 patterns were painted in yellow on the grey lids ($2\frac{1}{4}$ in. \times 4 in.) of food boxes set 12 in. apart on a horizontal shelf. Correct response consisted in pushing the lid with the square painted on it away from the cage to give access to the contents of the food box. A peanut could then be taken from the box and served as reward. Thirty trials were given each day and training was continued until the animal reached an arbitrary standard of performance. This standard consisted in making 10 or less errors in 100 consecutive trials. These last 100 trials are not included in the test scores, according to convention. The final score therefore represents the number of trials in excess of 100 required to achieve the standard level of performance (10 or less errors in 100 trials). The left/right positions of the positive cue (square) were randomized in accordance with a balanced schedule and non-correction procedure was used except in the rare event of a severe position habit (that is 10 consecutive responses to the same side). In that case the positive cue was maintained on the alternate side and the animal was allowed to correct 1 in 3 of its errors until no mistake was made on 3 consecutive trials. Such positional corrections were counted towards the daily total of 30 trials.

Animals were also tested informally and formally for the presence of field defects. In the formal test 11 peanuts were placed in line on a black horizontal shelf (19 in. \times 11 in.) set in front of the animal in the large wooden apparatus previously described. The animal was allowed to remove 3 nuts on each of 6 trials given on two different days. The position was recorded of each nut that the animal removed.

Sequence of operations and training.—Animals were allocated to a predetermined operative sequence at random. Details of the order and nature of the surgical procedures and of the training undertaken with each animal may be found in Table I. It will be seen that animals 1-6 learnt the discrimination preoperatively, whereas animals 7-12 had received 1 or 2 lesions before training began. The table also shows that every animal was required to relearn the discrimination after an interval of fourteen days' rest and before proceeding to the next operation whenever it had made more than 10 errors in the initial 100 trials of learning or post-operative re-learning. Up to three days elapsed between the end of a period of re-learning and the subsequent surgical intervention. No training was given on the pattern discrimination for a period of fourteen days following surgery. Informal charting of the visual fields was attempted by more than one observer during the first week after section of the left optic tract. The formal testing for field defects was carried out on the two days preceding surgery to the left optic tract and again between the tenth and thirteenth post-operative day.

RESULTS

Gross Behaviour Changes

A variety of neurological disorders and behaviour changes were observed as a result of the brain lesions. Thus following surgery to the

left optic tract there was a partial or complete ptosis of the left eye in animals 1, 6 and 9, and the heads of animals 5 and 6 were permanently held tilted to the right. A persistent right hemiparesis of varying severity (but mostly appearing to affect the leg more severely than the arm) came on in the case of animals 1, 2, 4, 5 and 6 as a consequence of the operation for section of the left optic tract. The immediate visual effects of this operation were not the same for all animals. Animals 1, 2, 4, 6 and 8 appeared to be totally blind for up to twenty-four hours after recovery from the anaesthetic. In contrast the remaining animals responded to visual as soon as to tactile and auditory stimulation. However all animals gave evidence of a complete homonymous hemianopia to the right on informal testing a few days after section of the left optic tract. This finding received subsequent support from the results on the formal test for field defects. For all animals, excepting only numbers 7, 9 and 11, after surgery selected significantly more nuts from the left end of the row than would be expected by chance, whereas choice was more evenly distributed between left and right ends before surgery (binomial test). As regards the 3 exceptional animals, number 7 was thought to have a left upper quadrant defect in addition to the right hemianopia.¹ Animal 11 continually sat in the front right-hand corner of the transport cage. Although it took nuts lying only to its own left, nevertheless these nuts formed part of the right end of the row owing to the animal's exceptional position.

For up to about five weeks following surgery most animals chose to make a three-quarter turn to the left rather than a quarter turn to the right when their attention was drawn in this direction. Moreover all animals that had previously used the right hand to take food without exception made use of the left following section of the left optic tract. In certain animals (numbers 2, 4, 5 and 6) the change from right to left hand preference could reasonably be attributed to the right hemiparesis. However no signs of paralysis were observed in animals 3, 7, 8, 9 and 11, and these likewise permanently changed their preference from right to left hand after section of the left optic tract.

In animals 4 and 12 the right optic tract was cut subsequent to section of the left tract to secure essential behavioural verification of the effectiveness of the earlier surgical procedure. Animal 4 was observed for twenty-four hours, animal 12 for forty-eight hours after section of the right tract. Although reactivity to auditory and tactile stimulation was regained after recovery from the anaesthetic and appeared to be intact neither animal ever again responded to visual stimulation. Moreover in both animals the pupillary light reflexes were absent in the two eyes throughout the period of observation. Animal 12 was able to walk

¹The left optic tract was seen on histological examination to be cut further medially and in closer proximity to the chiasm in this animal than in the others.

and climb well towards the end of the forty-eight hour survival period but failed to avoid obstacles.

Animal 9 suffered respiratory arrest and required artificial respiration during the operation for removal of the right frontal cortex. This animal was transiently blind (for about six hours) following surgery and persisted in circling to the left during the two-month period of survival. Such changes did not follow the larger frontal ablation in animal 7.

The operation for section of the corpus callosum was followed by a paralysis of the right leg and doubtful paralysis of the right arm in animal 3. No neurological changes were observed in animal 6 following a similar operation. However animal 8 became paralysed in the right leg on the third day after callosal section and developed frequent right-sided seizures on the fourth and fifth post-operative days, but not thereafter.

Pattern Discrimination

A summary of the findings on the pattern discrimination has been previously communicated elsewhere (Ettlinger, 1958). Full details of the number of trials required by every animal to achieve the standard level of performance at each stage of training are given in Table I.

Effect of single lesions on re-learning.—The range of the number of trials required to re-learn the discrimination following section of the left optic tract (animals 1-3) is 70-210. The range of the average number of errors per 100 trials of training ("average errors") is 21-26 for these 3 animals. In contrast animals 1-6 were all able to re-learn the discrimination in 0 trials (that is made 10 or less errors in the first 100 trials), with a range of average error of 0-3, when fourteen days had elapsed without surgical intervention. Therefore section of the left optic tract (animals 1-3) give rise to mild impairment in re-learning.

Animals 4-6 all re-learned the discrimination in 0 trials following a unilateral temporal ablation (range of average errors being 0-8). Therefore a unilateral temporal lesion (animals 4-6) gives rise to no impairment in relearning according to the measure of the number of trials.

Statistical comparison¹ between the effects of section of the left optic tract and ablation of one temporal region indicates a significantly greater retardation in relearning the discrimination following the former lesion ($p = 0.05$).

Effect of single lesions on initial learning.—Animals 7 and 8 required 1,050 and 440 trials to learn the discrimination for the first time after section of the left optic tract (average errors being 42 for both animals). In contrast animals 1-6 were able to learn the discrimination for the first

¹The Mann-Whitney test was used in this and all subsequent statistical comparisons.

TABLE I

Sequence of training and of operations for all animals. In this and the following tables the figures refer to the number of trials in excess of 100 required to reach the standard level of performance (10 or less errors in 100 trials) on the pattern discrimination. The symbol + indicates that the animal failed to reach the standard level of performance within the stated number of trials. — indicates that re-learning was not undertaken at this stage. The larger spacing between procedures represents the interval of fourteen days' rest between either (re-) learning or operation and subsequent (re-) learning. L signifies left-sided; R, right-sided; Tr, optic tract; Tm, temporal; Call, callosal; Fr, frontal.

Animal	1	2	3	4	5	6	7	8	9	10	11	12
Learning	510	340	280	200	430	390						
Re-learning	0	0	0	0	0	0						
1st operation:	L. Tr	L. Tr	L. Tr	L. Tr	R. Tm	R. Tm	L. Tr	L. Tr	L. Tr	R. Tm	L. Tr	L. Tr
(Re-) learning	210	80	70	0	0	0	1,050	440	690	780	480	1,140
Re-learning	0	0	0	—	—	—	10	0	0	0	0	0
2nd operation:	L. Tm	R. Tm	Call	L. Tr	L. Tr	Call	L. Tm	R. Tm	L. Tr	L. Tr	R. Tm	L. Tm
Re-learning	0	220	0	0	1,250+	0	0	150	80	450	380	510
Re-learning	—	0	—	—	—	—	—	0	0	0	20	0
3rd operation:	R. Tm	L. Tm	R. Tm			L. Tr	R. Fr	Call	R. Fr.	L. Tm		
Re-learning	1,250+	220	1,000+			1,250+	0	290	700	0		
Re-learning	0	0	0			0	—	0	0	20		

time in 200-510 trials prior to any surgical intervention (range of average errors being 31-42). Despite the overlap of scores there is then a suggestion that section of the left optic tract (animals 7 and 8) may give rise to impairment in learning ($p=0.07$).

Animals 9 and 10 required 690 and 780 trials to learn the discrimination following a unilateral temporal ablation (average errors being 45 and 43). Therefore a unilateral temporal lesion (animals 9 and 10) gives rise to impairment in learning ($p=0.036$).

Effect of two lesions.—Animals 4 and 9 required 0 and 80 trials to relearn the discrimination when the left optic tract was cut subsequent to a left temporal ablation (average errors being 3 and 11). Therefore section of the left optic tract subsequent to a left temporal lesion (animals 4 and 9) gives rise to no greater impairment than does section of the left optic tract alone (animals 1-3). Animals 1 and 7 both required 0 trials to re-learn the discrimination when the left temporal region was ablated subsequent to section of the left optic tract (average errors being 9 and 2). Therefore ablation of the left temporal region subsequent to section of the left optic tract (animals 1 and 7) gives rise to no greater impairment according to the measure of the number of trials than does ablation of one temporal region alone (animals 4-6).

Combining these results for animals 1, 4, 7 and 9, successive lesions to the left optic tract and left temporal region in either order are seen to give rise to no greater impairment in re-learning the discrimination than can be expected to follow section of the left optic tract by itself. These results are shown in Table II.

TABLE II

Effect of successive section of the left optic tract and ablation of the left temporal region upon re-learning of the pattern discrimination

Animal	1	4	7	9
	Learning			
	Re-learning			
1st operation	L. tract	L. temp.	L. tract	L. temp.
	Re-learning		Learning	
	Re-learning		Re-learning	
2nd operation	L. temp.	L. tract	L. temp.	L. tract
No. of trials to standard level of performance	0	0	0	80

Animal 5 required more than 1,250 trials and animal 10 required 450 trials to re-learn the discrimination when the left optic tract was cut subsequent to a right temporal ablation (average errors being 49 and 32). Therefore section of the left optic tract subsequent to a right temporal lesion (animals 5 and 10) gives rise to considerably greater impairment than does either section of the left optic tract alone (animals 1-3) or section of the left optic tract subsequent to a left temporal lesion

(animals 4 and 9). Animals 2 and 8 required 220 and 150 trials to re-learn the discrimination when the right temporal region was ablated subsequent to section of the left optic tract (average errors being 28 and 18). Therefore ablation of the right temporal region subsequent to section of the left optic tract (animals 2 and 8) gives rise to considerably greater impairment than does either a unilateral temporal ablation alone (animals 4-6) or a left temporal ablation subsequent to section of the left optic tract (animals 1 and 7).

Combining the results for animals 2, 5, 8 and 10 (see Table II), successive lesions to the left optic tract and right temporal region in either order are seen to give rise to significantly ($p=0.014$) greater impairment in relearning the discrimination than do successive lesions to the left optic tract and left temporal region (animals 1, 4, 7 and 9 of Table II).

TABLE III

Effect of successive section of the left optic tract and ablation of the right temporal region upon re-learning of the pattern discrimination

Animal	2	5	8	10
	Learning			
	Re-learning			
1st operation	L. tract	R. temp	L. tract	R. temp
	Re-learning		Learning	
	Re-learning		Re-learning	
2nd operation	R. temp	L. tract	R. temp	L. tract
No. of trials to standard level of performance	220	1,250+	150	450

Only 2 animals (numbers 11 and 12) learnt the discrimination for the first time after a left or right temporal ablation had already been combined with section of the left optic tract. The score of 480 trials for animal 11 (both lesions on the same side of the brain) falls within the range of scores obtained from unoperated animals (numbers 1-6) in learning the discrimination. The score of 1,140 trials for animal 1 (lesions on opposite sides of the brain) exceeds the scores of all other animals for initial learning.

Animals 3 and 6 both relearnt the discrimination in 0 trials when the corpus callosum was cut subsequent to a left optic tract section (animal 3) or right temporal ablation (animal 6) (average errors being 4 and 0). These scores may be compared with those achieved by animals 1-6 in re-learning prior to surgical intervention. Therefore section of the corpus callosum subsequent to a tract or temporal lesion gives rise to no impairment in re-learning according to the measure of the number of trials.

Effect of further lesions.—As shown in Table IV, animals 1, 7 and 10 required from 380 to more than 1,250 trials to re-learn the discrimination

when the right temporal region was ablated subsequent to both left optic tract and left temporal lesions (range of average errors being 33-51). Therefore ablation of the right temporal region subsequent to both left tract and left temporal lesions (animals 1, 7 and 11) would appear to give rise to greater impairment than does ablation of the same temporal region subsequent only to section of the left optic tract (animals 2 and 8, Table III).

TABLE IV

Effect of ablation of the right temporal region subsequent to both section of the left optic tract and ablation of the left temporal region upon re-learning of the pattern discrimination

Animal	1	7	11
Pre-existing lesions	L. tract L. temp	L. tract L. temp	L. tract L. temp
Further ablation	—	R. frontal R. temporal	—
No. of trials to standard level of performance	1,250+	840	380

As shown in Table V animals 2, 10 and 12 required from 0 to 510 trials to re-learn the discrimination when the left temporal region was ablated subsequent to both left optic tract and right temporal lesions (range of average errors being 10-22). Similarly animal 8 required 290 trials when the corpus callosum was cut subsequent to both left optic tract and right temporal lesions (average errors being 41). Therefore ablation of the left temporal region (animals 2, 10 and 12) or division of the callosum (animal 8) subsequent to both left tract and right temporal lesions would as a rule seem to give rise to greater impairment than can be expected to follow either ablation of the left temporal region (animals 1 and 7) or division of the callosum (animal 3) subsequent only to section of the left optic tract. On the other hand ablation of the left temporal region subsequent to both left tract and right temporal lesions (animals 2, 10 and 12, Table V) tends to give rise to less impairment than does ablation of the right temporal region subsequent to both left tract and left temporal lesions (animals 1, 7 and 11, Table IV).

TABLE V

Effect of ablation of the left temporal region or section of the corpus callosum subsequent to both section of the left optic tract and ablation of the right temporal region upon re-learning of the pattern discrimination

Animal	2	8	10	12
Pre-existing lesions	L. tract R. temp.	L. tract R. temp.	R. temp. L. tract	L. tract R. temp.
Further lesion	L. temp.	Callosal	L. temp.	L. temp.
No. of trials to standard level of performance	220	290	0	510

As shown in Table VI, animal 3 failed to re-learn the discrimination within 1,000 trials when the right temporal region was ablated subsequent to both left optic tract and callosal sections (average errors being 40). Similarly animal 6 failed to re-learn the discrimination within 1,250 trials when the left optic tract was cut subsequent to both right temporal and callosal lesions (average errors being 40). Therefore the combination of left tract and right temporal lesions subsequent to callosal section (animals 3 and 6) gives rise in these animals to considerably greater impairment than does the combination of left tract and right temporal lesions alone (animals 2, 5, 8 and 10, Table III).

TABLE VI

Effect of the combination of section of the left optic tract and ablation of the right temporal region subsequent to division of the corpus callosum upon re-learning of the pattern discrimination

Animal	3	6
First lesion	L. tract	R. temporal
Second lesion	Callosal	Callosal
No. of trials to standard level of performance	0	0
Further lesion	R. temporal	L. tract
No. of trials to standard level of performance	1,000+	1,250+

Animals 7 and 9 required 0 and 700 trials to re-learn the discrimination when the right frontal cortex was ablated subsequent to both left optic tract and left temporal lesions (average errors being 6 and 40). Therefore ablation of the right frontal cortex subsequent to both left tract and left temporal lesions gives rise to performance that is either superior (animal 7) or much inferior (animal 9) than that which can be expected to follow ablation of the right temporal region subsequent to section of the left optic tract (animals 2 and 8).

DISCUSSION

It has been shown that monkeys rendered hemianopic by section of the left optic tract make more errors in re-learning the pattern discrimination than do unoperated control animals. Hemianopic monkeys also tend to be retarded by comparison with unoperated animals in learning the discrimination for the first time. Under both conditions of learning the degree of impairment is generally slight. As all animals had some damage, varying in extent and location, of the medial part of the globus pallidus and of some fibres of the internal capsule in association with the section of the left optic tract it is not possible to ascribe any ensuing impairment on the pattern discrimination exclusively to section of the tract. Nevertheless the extent of the unintentional damage in these two structures varied from one animal to another, as did also the occurrence

of incidental damage in other structures in the neighbourhood of the left optic tract, without obvious correlation with the test performance. Similarly the degree of impairment subsequent to section of the left optic tract cannot be readily correlated with the presence or severity of a hemiparesis to the right. Nor yet was animal 1, which pre-operatively preferred the use of its left hand, less severely impaired than other animals which changed their preference from the right to the left hand following surgery. A similar alteration in hand preference favouring the hand on the side of the remaining intact visual half-field has been previously reported as a result of striate lesions in monkeys by Klüver (1937) and Settlage (1939). At any rate the majority of errors were made by the hemianopic animals when the positive cue was placed to the side of the blind right half-field. It would then seem reasonable to relate the deficit in these animals to a transient failure of visual searching towards the right. The animals had to learn to look actively for an alternative cue when the negative pattern was presented in the intact left half-field. This visual search was initially achieved by a three-quarter turn to the left, and only later by a head movement to the right.

The present results serve to confirm previous reports (e.g. Mishkin and Pribram) that a visual discrimination may be re-learned in as few trials after a period allowed for recovery from a unilateral infero-temporal ablation as after an equal interval without surgical intervention. However, initial learning of the pattern discrimination was shown to be retarded after ablation of either the left or right temporal region. This finding accords with other evidence (Mishkin and Hall) that bilateral temporal lesions give rise to greater impairment when a discrimination is learnt for the first time following surgery than when it is first learnt before and then re-learned after the lesions are made. Therefore re-learning is more obviously disrupted than is initial learning by section of one optic tract whereas the converse result is the rule after a unilateral temporal ablation. Such contrasting effects of the two kinds of lesion provide some measure of support for the findings of Wilson and Mishkin, who compared the behaviour of animals with striate and temporal ablations and also reported a dissociation in the effects of the lesions.

It is of some interest that a unilateral temporal ablation consistently gives rise to defective re-learning of the pattern discrimination when it is placed on the side of the brain opposite to a section of the optic tract, but fails to do so when these two lesions are both placed on the same side of the brain. There is no overlap between the scores of animals with left tract and right temporal lesions on the one hand, and of animals with left tract and left temporal lesions on the other. It might be claimed that the deficit of the former group is the result of non-specific interaction between lesions on opposite sides of the brain, and not primarily the result of temporal involvement. This possibility cannot be entirely

rejected on the present findings. Two lines of evidence would, however, tend to contra-indicate such an argument. Firstly, combined left tract and right frontal lesions (in addition to left temporal ablations) give to either smaller (animal 7) or to greater (animal 9)¹ impairment than combined left tract and right temporal lesions. Secondly, the combination of left tract and right temporal lesions subsequent to division of corpus callosum disrupts re-learning of the discrimination at least as severely as does the ablation of both left and right temporal regions.

It would then appear from these results that there is a preferential relationship between a given infero-temporal region and behaviour dependent upon the primary visual inflow to the *same* hemisphere (if the assumption is made that each temporal region ultimately interacts with the visual inflow or its derivations during visual discrimination, then each temporal region would appear to interact preferentially with the inflow or its derivatives arriving in the *same* hemisphere). For example, if the left temporal region were as intimately related to behaviour dependent upon the visual inflow to the right as to behaviour dependent upon the visual inflow to the left hemisphere, then a left temporal ablation would be expected to disrupt visual discrimination as severely as a right temporal ablation when the visual inflow is restricted (by section of the left optic tract) to the right hemisphere. The present evidence would then suggest that the disorder of visual discrimination consequent upon bilateral temporal lesions in monkeys does not occur at so high a level of visual perception as to be quite independent of laterality.

However, it had been originally predicted (on the assumption that ablation of each temporal region gives rise to a qualitative change in visual efficiency in the contralateral half visual field) that combined lesions to the left optic tract and right temporal regions would impair visual discrimination as severely as combined left and right temporal ablations. Animals with left tract and left temporal lesions were therefore subjected to ablation of the right infero-temporal region. More trials were then required by all of these animals to re-learn the discrimination than by other animals which had the right temporal region ablated subsequent only to section of the left optic tract. The inference would therefore seem inescapable that preservation of the left temporal region minimizes the impairment consequent upon combined left tract and right temporal lesions.

An extension of this inference is legitimate on the basis of the further finding that 2 out of 3 animals were impaired when the left temporal region was ablated subsequent to both left tract and right temporal lesions (animals 2 and 12). This result runs contrary to any interpretation

¹As already reported above animal 9 may have become severely anoxic during operation for removal of the right frontal cortex.

tion of the visual disorder in temporal monkeys as being secondary to damage to any part of the primary visual afferent system. For the visual deficit ensued in these two animals as a consequence of a temporal lesion to a hemisphere in which the visual afferent system had already been totally inactivated by section of the optic tract. Behavioural verification of the total blockage of visual afferents to the left hemisphere was forthcoming in the case of animal 12 (which suffered the greater visual deficit). For it was rendered completely blind by eventual section of the right optic tract. It would therefore seem to be the case that, *provided the opposite temporal region has previously been destroyed*, each infero-temporal region can become concerned in behaviour dependent upon the visual inflow to the opposite hemisphere. Such a relationship so to speak "across the brain" would not, however, appear to be ever as effective as is that within one hemisphere (compare Tables IV and V).

The connecting pathways by means of which each infero-temporal region might ultimately interact with the visual inflow or its derivatives in discrimination learning are not known. Collicular, thalamic and direct occipito-temporal cortical circuits have all been rejected on experimental evidence. Some information on this point could be gained in the present study. In monkeys with combined left tract and right temporal lesions no visual inflow (primary or derivative) is known to reach the left hemisphere except from the right striate area through the corpus callosum. Bremer and Stoupe (1956) have obtained electrophysiological evidence for the interaction of the two striate areas by this route on stimulation of one lateral geniculate body. Division of the corpus callosum would then serve to abolish all known visual inflow to the left hemisphere. As a result even those extra-temporal regions of the left hemisphere which, with homologous areas on the right, must be assumed to take over the functions of the temporal sector after bilateral temporal ablations, would be isolated. Total section of the corpus callosum in combination with appropriate other lesions as shown in Tables V and VI¹ does in fact afford support for the view that the left temporal region is dependent upon visual messages that pass from the right to the left striate area through the corpus callosum after destruction of the right temporal region. Further pathways between the left striate and temporal regions may then be presumed to exist, even though perhaps involving multiple synapses. It would seem reasonable to suppose that these same occipito-temporal pathways are in use when visual inflow arrives at each striate area directly in the intact animal. However it

¹The severity of the impairment resulting from combined left tract and right temporal lesions subsequent to section of the callosum is especially noteworthy; it is thought to follow from isolation of both temporal and extra-temporal areas of the left hemisphere. In contrast animal 8 of Table V had been impaired following the first two lesions, so that the right extra-temporal region may have already assumed temporal functions before the callosal section.

cannot be claimed with certainty on the basis of the present results that the corpus callosum is concerned with visual discrimination in the intact monkey.

Some further implications follow from the present results. Firstly successive variation of the neurological status of the animal by means of serial lesions under constant conditions of behavioural observation has been shown to be of value in the analysis of behaviour changes resulting from brain lesions (cf. also Chow and Survis, 1958). This method is however, merely complementary to other procedures in which test conditions are systematically varied in conjunction with only one change in neurological status. Secondly it would appear that the action of the region within the "association cortex" of the monkey known to be concerned with visual performance has been delimited somewhat more clearly. For this region has been shown to influence visual discrimination not by direct interaction at any level with the geniculostriate afferent system. Rather, it would seem to be concerned with visual messages proceeding from the striate areas, and in such a way that the temporal region on each side of the brain is predominantly, but not invariably, related to the messages leaving the striate area of the same hemisphere.

The recent findings of Mishkin (1958) who has combined unilateral lateral temporal ablations with striate removals in the same or opposite hemisphere and with section of the corpus callosum, although as yet only reported in abstract afford confirmation of many of the results presented in this paper.

SUMMARY

The behavioural manifestations of a visual disorder that follows bilateral inferior temporal lesions in the monkey are described, and the relevance to perceptual disturbances in man are discussed. It is argued that the possible contribution of areas of amblyopia in the genesis of this disorder in monkeys has not been adequately examined.

An investigation of the effects of various successive lesions on the ability to learn and retain a visual pattern discrimination was undertaken in 12 monkeys. The findings suggest that in the monkey the inferior temporal regions influence visual discrimination behaviour not by direct interaction at any level with the primary visual afferent system, but rather by interaction with messages proceeding from the striate areas. It has also been shown that each infero-temporal sector is preferentially related to behaviour dependent upon the primary visual inflow to the same hemisphere, although a given sector may interact with messages proceeding from the opposite striate area via the corpus callosum provided that the opposite temporal area has previously been ablated.

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