

D-4

Reprinted from THE JOURNAL OF COMPARATIVE NEUROLOGY
Vol. 93, No. 1, August 1950

A BEHAVIORAL ANALYSIS OF THE ORGANIZATION OF THE PARIETO-TEMPORO-PREOCCIPITAL CORTEX

JOSEPHINE SEMMES BLUM, KAO LIANG CHOW AND
KARL H. PRIBRAM

*Yerkes Laboratories of Primate Biology and Yale University
Orange Park, Florida and New Haven, Connecticut*

FOURTEEN FIGURES

INTRODUCTION

The experimental literature dealing with cortical mechanisms of complex behavior has been largely preoccupied with the frontal granular region. One recent writer (Halstead, '47) has even ventured to call this sector, "the organ of civilization." Yet, if there is any characteristic which distinguishes man from even the highest primate, it is the possession of propositional language. The fact that lesions in the posterior areas of the brain result in aphasias and related disturbances demonstrates that these regions share in the mediation of human intelligent behavior.

Research on the posterior part of the cortex has in most cases been undertaken either to provide controls for frontal ablations or to study elementary sensory capacities. In the former type of study, lesions in the posterior regions have usually been found to produce little, if any, disturbance. There are several considerations, however, which make it necessary to reexamine the hypothesis of unique potency of the frontal lobes. Although great emphasis has been placed on the phylogenetic increase in the relative size of the frontal granular cortex, von Bonin ('41) points out that there is actually no significant difference in the relative size of the frontal lobes between man and chimpanzee, but that man's mental superi-

ority may to some extent be explained by the relative increase of the parietal and temporal lobes. Failure of experimental ablations of the posterior neocortex to produce serious behavioral defects may have been caused by the fact that, whereas the frontal granular areas have been considered a unit and ablated as such, the posterior granular cortex (exclusive of sensory projection areas) has been subdivided into parietal, temporal, and preoccipital parts, these being removed separately. As a consequence, either the mass of tissue removed may have been less, or, if the parieto-temporo-preoccipital complex acts as a unit, the removal of any of these subdivisions may have been insufficient to derange the function of the whole. Another consideration is that, in human cases, bilateral involvement limited to the frontal granular cortex is not uncommon (e.g., olfactory groove meningiomas, trauma), whereas similar bilateral destruction posteriorly is a rarity.

The most striking alterations of behavior following experimental cerebral ablations have resulted from lesions outside the frontal granular cortex, i.e., from temporal lobectomy (Klüver and Bucy, '38). The syndrome produced by this removal includes such diverse abnormalities as "psychic blindness," "oral tendencies," "tameness," and "hypersexuality." It has been suggested that the visual symptoms may have resulted from involvement of area 19 (Fulton, '43). It seems improbable that the functions implied by these symptoms have such a restricted locus in view of the negative findings following extensive preoccipital removals (Lashley, '48; Chow, '50). Either a wider area of cortex mediates these functions, or a critical focus exists somewhere in the temporal region. Furthermore, it seems from the descriptions given by Klüver and Bucy that the "psychic blindness" was not restricted to the visual sphere, since tactile recognition of objects was apparently also deficient. The finding that extensions of parietal lesions into the posterior part of the temporal lobe produce more severe somatosensory deficit than posterior parietal lesions alone (Blum, '50) also supports the view that the parieto-temporo-preoccipital region as a whole may par-

ticipate in somatosensory, visual, and possibly other capacities. No clear cytoarchitectural boundaries can be established within this region (Lashley and Clark, '46), except the differentiation of allocortex from neocortex in the temporal lobe.

All these lines of evidence indicate the need of a comparison of the effects of ablation of the parieto-temporo-preoccipital neocortex as a unit with those produced by lobectomies made according to the conventional distinction of parietal and temporal lobes. We have therefore prepared a series of monkeys with lesions involving a combination of the parietal, temporal and preoccipital areas; animals with parietal or with temporal lobectomies served as controls. Other studies (Blum, '50; Chow, '50) of the effects of sub-total lesions in the parieto-temporo-preoccipital region provide additional controls, which will be considered in relation to the results of the present experiment. In order to clarify the nature of the functions disturbed, tests were selected and observations made to detect sensory deficit in vision, somesthesia, audition, and gustation, disturbances of integrative processes, or alterations in the affective-reactive aspects of behavior.

MATERIAL AND METHODS

Six immature rhesus monkeys (*Macaca mulatta*) were used. Their weights ranged from 2 to 2.3 kg. They were observed and trained preoperatively on visual, somesthetic, auditory and gustatory tasks, as well as on conditional and delayed reaction problems. Their levels of activity and general behavior were noted. In 4 of these monkeys (PTO-1, PTO-2, PTO-3, and PTO-4), the region between the postcentral gyrus and the lunate sulcus, including the lateral surface of the temporal lobe, was removed bilaterally. For purposes of comparison, a bilateral temporal lobectomy was made on a 5th monkey (T-1), and a bilateral parietal ablation on another (P-1).¹ All operations were done in two stages. Two weeks after the second operation formal training and testing was resumed. After

¹The letters PTO designate the parieto-temporo-preoccipital removal; T, the temporal lobectomy; and P, the parietal excision.

completion of postoperative testing, the animals were sacrificed. Their brains were fixed and sectioned, reconstruction was made of the cortex, and thalamic degeneration recorded.

Subjects

PTO-1, male. Predominantly left-handed. Lateral surface of the left parieto-temporo-preoccipital region removed, 4/15/48. Symmetrical removal on the right, 4/23/48. Trained and tested preoperatively and postoperatively in all problems. Sacrificed, 8/18/48.

PTO-2, male. Predominantly right-handed. Lateral surface of right parieto-temporo-preoccipital region removed, 2/26/48. Symmetrical removal on the left, 3/11/48. Trained and tested preoperatively in all problems, except auditory discrimination, taste preference, and conditional reaction. Postoperative data were obtained on all problems in which he was preoperatively trained, except delayed reaction and patterned string problems. Accidental death, 5/7/48.

PTO-3, male. Predominantly left-handed. Lateral surface of the left parieto-temporo-preoccipital region removed, 4/2/48. Symmetrical removal on the right, 4/17/48. Trained and tested preoperatively and postoperatively in all problems. Subsequent bilateral removal of frontal granular cortex (behavioral effects of this operation to be reported elsewhere). Sacrificed, 3/8/49.

PTO-4, male. Predominantly right-handed. Lateral surface of the right parieto-temporo-preoccipital region removed,² 4/5/48. Removal on the left, 4/19/48. Trained and tested preoperatively and postoperatively in all problems, except taste preference. Subsequent bilateral removal of frontal granular cortex (behavioral effects of this operation to be reported elsewhere). Sacrificed, 3/14/49.

²At operation, a cranio-cerebral scar, slightly greater than 1 cm in diameter, was found in the upper part of the right angular gyrus. Grossly, the scar appeared old, and probably resulted from an injury in infancy. It was removed as part of the planned excision.

T-1, female. Predominantly left-handed. Removal of the left temporal lobe, 4/22/48. Symmetrical removal on the right, 5/1/48. Trained and tested preoperatively and postoperatively in all problems. Sacrificed, 12/4/48.

P-1, male. No consistent preference for either hand. Right parietal lobectomy and partial preoccipital excision, 7/27/48. Symmetrical removal on the left, 8/11/48. Trained and tested both preoperatively and postoperatively only on somesthetic problems. In addition to the somesthetic problems, he was trained postoperatively on visual color and pattern discriminations and on delayed reaction. Sacrificed, 2/10/49.

Operations

Under nembutal anaesthesia, the lateral surface of the hemisphere was exposed from the central fissure to well beyond the lunate sulcus and from the midline down to the inferior temporal convolution. Incisions were made in a relatively avascular portion of the gyrus to be removed, and bleeding was controlled by packing with cottonoid patties. The cortex of the gyrus and of the adjacent banks of the sulci was then resected by subpial suction. Each gyrus was handled separately in this manner so as to remove a maximum of cortex with minimal damage to underlying white matter. In the case of the temporal lobectomy, the excision was extended through the white matter to include the medial surface. The cautery was used to interrupt the vein of Labbé. Wounds were sutured in anatomic layers.

Histological procedures

The cerebral hemispheres were fixed in 10% formalin and sketched under camera lucida. They were then dehydrated in alcohols, and embedded in nitrocellulose. They were cut into serial coronal sections of 50 μ thickness; every 10th section was saved and stained with thionin. The surface extent of the

lesions was determined from sections and translated by orthogonal projection to the original proportions of the hemispheres, as shown in the camera sketches. Representative sections were selected to illustrate the depth of the excisions. Retrograde degeneration in thalamic nuclei was studied. Regions where nerve cells had disappeared, or become obviously less numerous, or where glia had markedly increased, were considered clear instances of retrograde degeneration and were outlined on drawings of the sections through the thalamus. Degeneration was called "doubtful" if the neurons merely appeared swollen or pale, or if there was only slight gliosis. Our first category, that of clear or certain degeneration, is defined by the most generally accepted criteria of retrograde thalamic degeneration. The cause of the difference between this kind of degeneration and that we have termed "doubtful" is unknown. The latter may possibly be transneuronal, rather than retrograde, or caused by damage to axon collaterals.

Tests

We have divided the tests and observations into three categories: those of relatively simple sensations and perceptions ("tests of sensation-perception"), those of so called "higher" mental functions ("tests of ability to respond differentially according to context"), and those of the affective-reactive aspects of behavior ("observations of activity and temperament").

Under the first category, we include tests of visual, somesthetic, gustatory, and auditory abilities. In the visual sphere, observations and tests of visual pursuit, extent of the visual field, acuity, depth perception, orientation, differentiation of food from inedible objects and of fear-provoking from innocuous stimuli, recognition of familiar objects, color discrimination, pattern discrimination, and ability to solve patterned string problems are made. The procedures used in making these tests are described in Chow ('50), except for the string patterns, which are those used by Lashley ('48). The appa-

ratus and general procedure used in the somesthetic tests has been reported by Blum ('50). The discrimination problems require reaction to differential sizes (circles, 3.8 cm and 1.9 cm in diameter), forms (rectangle, 4.3×2.5 cm *vs.* equilateral triangle, 4.3 cm high), roughnesses (grade 3 *vs.* grade 0000 sandpapers), or weights (170 gm *vs.* 30 gm). The auditory tests have been described (Chow, '50). In the tests of gustation, choice is offered between water and a bitter solution and between banana and meat or fish. For the former, the apparatus used is a modification of that employed by Patton and Ruch ('44). Attached to the monkey's living cage are two funnels containing water and two containing a quinine solution. The positions of the 4 funnels are interchanged in a random order from day to day. The quinine solutions used are .1%, .025%, .0062%, and .0015%, given in that order. Each concentration is offered for two days, and the amount consumed in a 24-hour period recorded (corrected for evaporation).

The second category includes conditional reaction and delayed reaction problems. These tests are here grouped together, because of the similarity of their requirements for shift of direction of reaction in accord with another cue (color of background in the former and position of previous exposure of the reward in the latter). Procedures are described in Chow ('50).

Observations in the third category are those of level of gross activity (measured with a pneumatic recording device attached to the living cage), and of general behavior in the home cage and in the test situation.

EXPERIMENTAL RESULTS

Immediate postoperative effects

After the first operation there were contralateral homonymous visual field defects in all animals lasting from two days to two weeks; these defects had become undetectable by the

time of the second operation. All animals reacted normally to interoperative tests of differentiation of food from inedible objects. There were signs of contralateral decrease in tactile sensibility in all animals except the one with the temporal lobectomy. The contralateral limbs were weak and tended not to be used by these animals, or to be used in an awkward fashion. These symptoms were especially prominent in the monkey with the large parietal ablation (P-1). Inaccuracies of reach appeared in subjects PTO-3, PTO-4, and P-1.

The second operation caused an apparent total blindness in subjects PTO-2, PTO-3, and P-1. Vision began to return in the field ipsilateral to the second operation within the first week and was apparently normal by the end of the second week. There were only contralateral field defects in the other subjects and these disappeared during the first few postoperative days. Animals PTO-2, PTO-3, PTO-4, and T-1 picked up and orally manipulated food and inedible objects indiscriminately. By the end of the first postoperative week animals PTO-4 and T-1 were normal on this test; animals PTO-2 appeared normal on the 11th day, but later reverted to indiscriminate behavior. Somatosensory defects were contralateral, except in P-1 in whom the second operation caused a recurrence of symptoms on the ipsilateral side. Grasping with either hand was never again normal in this animal during the period of observation, though his gross locomotor disabilities disappeared in the first few weeks.

Test results

The results given in this section are those which were obtained after the recovery period of 14 days. Symptoms which disappear within the recovery period may be reasonably ascribed to non-specific operative trauma (edema, shock, etc.), whereas the more lasting changes in behavior, which we present here, are probably ascribable to specific and permanent brain damage.

I. Tests of sensation-perception.

A. Visual functions.

1. Controlled observations of visual abilities.

Visual pursuit: None of the animals tested, except PTO-3, showed any postoperative change in this ability. This animal did not show appropriate eye movements in following food rapidly moved into the upper half of the visual field, though lateral pursuit was unchanged. (P-1 was not tested for this and many of the following abilities, because our principal interest in P-1 involved comparative effects on somesthetic and visual discrimination learning.)

Extent of the visual field: No constriction of the field was detected in any animal, except PTO-3, who neglected food introduced into his right upper visual field.

Visual acuity: No decrease of visual acuity was found, except in PTO-2 and PTO-3. PTO-3 failed to respond at all to the two finest black threads (.08 and .15 mm in diameter), and on the coarsest black thread (.4 mm), gave only three out of five possible responses. PTO-2 responded only three times out of five opportunities to the two finest black threads. Response to the white threads was not altered in either subject. P-1 was not tested.

Depth perception: The threshold value (about 1 cm at a distance of 15 cm) was unchanged. P-1 was not tested.

Differentiation of food from inedible objects: After the first week following operation, no abnormalities were noted, except in PTO-2 and PTO-3. The performance of PTO-2 was normal on the 11th postoperative day, but he failed to discriminate thereafter. The last test was given on the 32nd day. PTO-3 did not discriminate until several months after operation. Success on this test in PTO-1, PTO-4, and T-1 was obviously achieved on the basis of visual cues, for there was no manipulation of the objects prior to choice. P-1 was not tested.

Differentiation of fear-provoking from innocuous stimuli: Of the 5 animals tested, three (PTO-2, PTO-3, and T-1) failed

postoperatively to show any emotional reaction to a live snake or to other objects which are normally avoided. T-1 even attempted to pick up the snake. By the end of three months, T-1 showed the normal fear reaction; PTO-2 and PTO-3 were not tested after 6 weeks. P-1 was not tested.

Orientation: None of the animals was disoriented in its home environment, except PTO-2 and PTO-3, especially the

TABLE 1

Color discrimination

Trials and errors required to reach a criterion of 20 successive errorless trials within a 30-trial session on the discrimination of a red from a green square stimulus plaque on a black tray. (This discrimination was used as Condition A in the conditional reaction problem)

Scores in parentheses indicate failure to reach the criterion

SUBJECT NO.	PREOPERATIVE		POSTOPERATIVE	
	Trials	Errors	Trials	Errors
PTO-1	110	37	270	74
PTO-2	30	13	(500) failed	(268)
PTO-3	150	41	545	193
PTO-4	61	20	152	78
T-1	140	52	424	143
P-1 ¹			159	54

¹ Subject P-1 was tested only postoperatively.

former. They had to be guided into the carrying cage and back into their living quarters. This condition persisted for one to two months after operation but eventually disappeared.

2. Tests requiring formal training.

No animal required readaptation to the visual problem situation *per se*, except PTO-2. This animal appeared unable in the first few sessions to find the discriminanda, although he groped and fumbled about the tray on which they were presented. Both PTO-2 and PTO-3 at first had difficulty in find-

ing the food reward after the stimulus plate had been displaced.

Color discrimination: (table 1). After operation, all animals lost the habit of differential reaction to red and green. They were also retarded in the rate of relearning this discrimination, requiring about two to four times the number of preoperative trials, although, with the exception of PTO-2, the

TABLE 2
Discrimination of painted patterns

Trials and errors required to reach a criterion of 20 errorless successive trials within a 30-trial session on the discrimination of a black diamond painted on a white background from black and white horizontal striations. The stimulus plaques were identical in size, shape, and relative area of black and white

SUBJECT NO.	PREOPERATIVE		POSTOPERATIVE	
	Trials	Errors	Trials	Errors
PTO-1	120	43	272	111
PTO-2	325	132	(500) failed	(223)
PTO-3	180	54	(500) failed	(212)
PTO-4	120	68	450	161
T-1	120	24	530	162
P-1 ¹			60	19

¹ Subject P-1 was tested only postoperatively.

habit was eventually reacquired.³ P-1 was the only animal not trained preoperatively; his postoperative learning score was not significantly different from those of normal monkeys.

Discrimination of painted patterns: (table 2). All animals lost this habit. However, with the exception of PTO-2 and

³ It might be thought that postoperative loss of the discriminative reaction to colors resulted from the possible confusion occasioned by the preoperative training in conditional reaction, of which this color discrimination was the basis. However, Chow ('50) showed that loss of the color discriminative habit follows temporal lesions, even when the monkey is not trained preoperatively on conditional reaction.

PTO-3, all relearned, although they required two to four times the number of preoperative trials. P-1 was the only animal not trained preoperatively; his postoperative learning score was not significantly different from those of the normals.

Patterned string problems: Two of the monkeys (PTO-2 and P-1) were not tested on these problems. All others showed postoperative deficit, either by requiring more trials, or failing to reach the criterion on some or all of the problems solved preoperatively.

TABLE 3
Size discrimination (somesthetic)

Trials and errors required to reach a criterion of 20 successive errorless trials on the discrimination of circles, 3.8 cm and 1.9 cm in diameter, respectively. Postoperative scores in italics are those made with the postoperatively preferred hand

SUBJECT NO.	PREOPERATIVE				POSTOPERATIVE			
	Right		Left		Right		Left	
	Trials	Errors	Trials	Errors	Trials	Errors	Trials	Errors
PTO-1	185	47	79	<i>25</i>	52	9
PTO-2	192	50	<i>119</i>	<i>33</i>
PTO-3	98	15	<i>205</i>	<i>45</i>	132	29
PTO-4	83	19	317	91	<i>183</i>	<i>47</i>
T-1	115	19	178	30	<i>46</i>	<i>10</i>
P-1 ¹	320	78	103	13

¹P-1 used either hand both pre- and postoperatively.

B. Somesthetic tests.

Because of shifts in the animals' preferential use of the hands following operation, the results of tests of somesthetic functions are complicated. The second operation was in every case done on the hemisphere contralateral to the hand trained on the discrimination problems (except for P-1, who showed no exclusive hand preference pre- or postoperatively). After operation, all animals of the PTO group spontaneously used the *untrained* hand in the discrimination box. PTO-2 resumed his original hand preference during the readaptation period,

but the others persisted in the use of the untrained hand. In the first postoperative tests, the animals were allowed to use their preferred hands, even though that hand had not been used in the somesthetic discrimination problems during preoperative training. Thus the first postoperative score on each problem was, for three of these animals (PTO-1, PTO-3, and PTO-4), obtained with the previously untrained hand. P-1 continued to use either hand, although the hand ipsilateral to the second operation was used more than the other. T-1 did not shift handedness.

After the criterion had been reached on each of the problems with the postoperatively preferred hand, PTO-1, PTO-3, and PTO-4 were forced to use the hand which had been preoperatively trained by restraining the other with a short chain attached to a waist belt. T-1 was also tested in this way, but since the hand he was forced to use had not been trained preoperatively and was not preferred postoperatively, these results are not comparable to those of the PTO group.

Before formal postoperative training could be begun, all animals, except T-1, required almost as much adaptation to the use of the tactile discrimination box as they required originally. In the PTO animals, there was apparently an amnesia for the problem situation *per se*, a result which contrasts with their behavior toward the apparatus for visual discrimination training. At first, these animals had to be taught even to reach into the box; then, to find the food cans visually. With vision excluded, they were again disoriented as to the location of the stimulus-objects, but all finally regained adequate kinesthetic orientation. P-1 appeared less disoriented than the PTO group, but had difficulty in learning to grasp the stimulus-objects properly in order to remove them from the food cans. T-1 required no readaptation at all.

Size discrimination: (table 3). Using the preoperatively trained hand, all animals, except PTO-3 and PTO-4, required fewer trials to relearn this discrimination than originally. PTO-3 and PTO-4 lost the habit and were retarded in relearning it, the former requiring only a slightly increased num-

ber of trials but the latter about 4 times the preoperative number.

With the preoperatively untrained hand, PTO-3, PTO-4, and T-1 required more trials than originally, but PTO-1 showed saving. It is significant that in the latter case, the habit was transferred to the previously untrained hand.

Form discrimination: (table 4). Using the preoperatively trained hand, all animals, except PTO-1 and PTO-4, showed

TABLE 4
Form discrimination (somesthetic)

Trials and errors required to reach a criterion of 20 successive errorless trials on the discrimination of a rectangle from a triangle, of equal surface area. Post-operative scores in italics are those made with the postoperatively preferred hand

SUBJECT NO.	PREOPERATIVE				POSTOPERATIVE			
	Right		Left		Right		Left	
	Trials	Errors	Trials	Errors	Trials	Errors	Trials	Errors
PTO-1	378	160	<i>297</i>	<i>116</i>	581	217
PTO-2	126	48	<i>123</i>	<i>39</i>
PTO-3	519	205	<i>273</i>	<i>67</i>	376	164
PTO-4	628	285			(840)	(380)	<i>302</i>	117
					failed			
T-1	852	277	255	87	<i>298</i>	<i>62</i>
P-1 ¹	644	284	359	102

¹ P-1 used either hand both pre- and postoperatively.

saving in trials to relearn. PTO-1 and PTO-4 lost the habit. In the former animal, the habit was regained (although at a somewhat slower rate than preoperatively), while in the latter, there was failure to relearn within the limits of training.

With the preoperatively untrained hand, all animals tested required fewer trials than originally to learn this discrimination. Thus, in this problem all three subjects who shifted handedness gave evidence of transfer of the learned discriminative reaction to the other hand.

Roughness discrimination: (table 5). Using the preoperatively trained hand, 4 of the 6 animals lost the habit (T-1, P-1, PTO-3, and PTO-4). T-1 was able to regain it at a normal learning rate, but the latter three animals failed to relearn. In contrast, PTO-1 and PTO-2 showed saving.

With the preoperatively untrained hand, T-1 failed to learn within the limits of training, but the three animals of the PTO

TABLE 5
Roughness discrimination (somesthetic)

Trials and errors required to reach a criterion of 20 successive errorless trials on the discrimination of grade 3 and grade 0000 sandpaper. Postoperative scores in italics are those made with the postoperatively preferred hand

SUBJECT NO.	PREOPERATIVE				POSTOPERATIVE			
	Right		Left		Right		Left	
	Trials	Errors	Trials	Errors	Trials	Errors	Trials	Errors
PTO-1	692	233	<i>141</i>	<i>36</i>	168	30
PTO-2	345	134	<i>321</i>	<i>88</i>
PTO-3	294	82	<i>128</i>	<i>40</i>	(510)	(223) failed
PTO-4	329	97	(510)	(221) failed	<i>155</i>	<i>29</i>
T-1	237	84	(750) failed	(246) failed	<i>246</i>	<i>81</i>
P-1 ¹	538	161	(660) failed	(272) failed

¹ P-1 used either hand both pre- and postoperatively.

group who were tested acquired the habit in fewer trials than originally. Here again is evidence of habit transfer in the animals who shifted handedness.

Weight discrimination: (table 6). Using the preoperatively trained hand, three of the six animals lost the habit (PTO-3, PTO-4, and P-1). PTO-3 was slightly retarded in relearning it, and the latter two animals failed to relearn. In contrast, PTO-1 and PTO-2 showed saving. T-1 failed to meet the

criterion both pre- and postoperatively, but his level of performance (about 70% correct) was not significantly altered after operation.

With the preoperatively untrained hand, PTO-3 and PTO-4 required about 25% more trials than originally to learn this discrimination, but PTO-1 showed saving.

TABLE 6
Weight discrimination (somesthetic)

Trials and errors required to reach a criterion of 20 successive errorless trials on the discrimination of a 170 gm weight from 30 gm weight. Postoperative scores in italics are those made with the postoperatively preferred hand

SUBJECT NO.	PREOPERATIVE				POSTOPERATIVE			
	Right		Left		Right		Left	
	Trials	Errors	Trials	Errors	Trials	Errors	Trials	Errors
PTO-1	619	164	<i>283</i>	<i>59</i>	<i>253</i>	<i>71</i>
PTO-2	365	95	<i>168</i>	<i>27</i>
PTO-3	442	155	<i>538</i>	<i>150</i>	627	189
PTO-4	361	87	(750)	(330)	<i>415</i>	<i>148</i>
					failed			
T-1	(1189)	(441)	(500)	(167)
					failed			failed
P-1 ¹	526	126	(750)	(247)
					failed			

¹ P-1 used either hand both pre- and postoperatively.

Summary of results: Considering the somesthetic tests as a group, it appears that PTO-4, PTO-3, and P-1 were the animals most severely affected by the operations. With the preoperatively trained hand, PTO-4 was retarded, or failed, on every problem; PTO-3, on three of the four problems; P-1, on two of the four problems. PTO-1 lost one habit and was retarded in relearning it; T-1 lost one habit and regained it at a normal rate; PTO-2 showed some retention, as measured by saving, on every test.

nucleus, except for a narrow strip along the medial margins of the posterior part of n. pulvinaris.

Parietal lesion: The posterior extent of the lesion in P-1 (figs. 13 and 14) included both banks of the lunate sulci, but

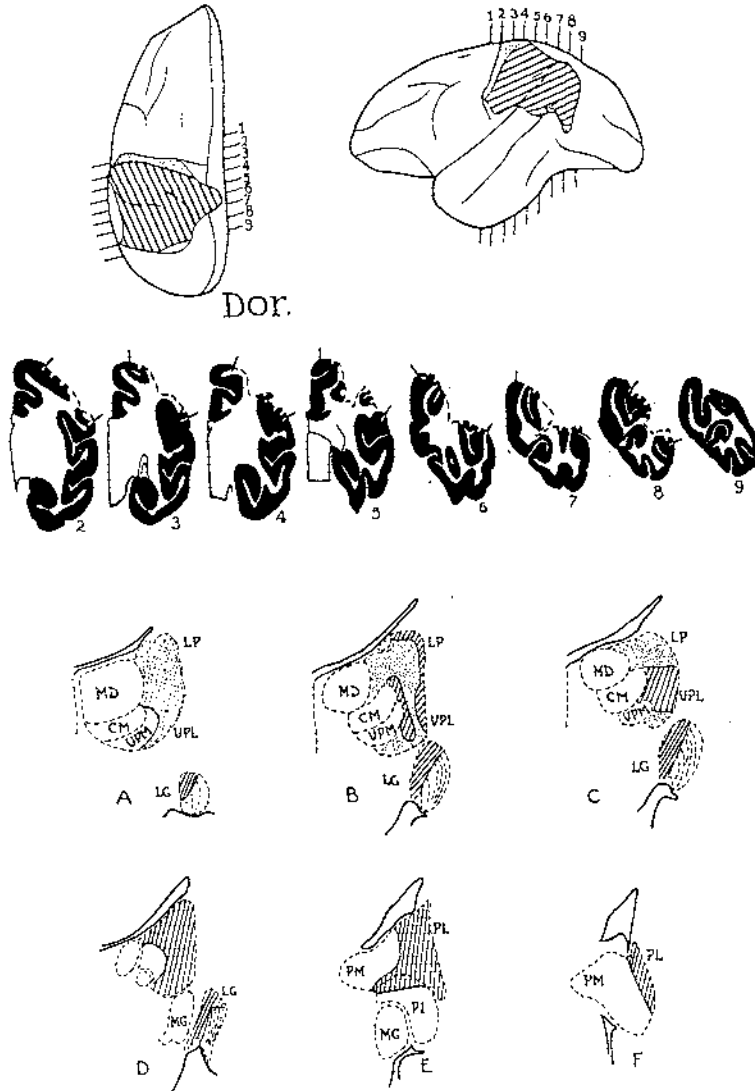


Fig. 13 Record of lesion in the left hemisphere of P-1.

invaded the striate cortex only minimally. Anteriorly, the lesion included most of the postcentral gyrus, involving the posterior bank of the central fissure bilaterally. Superiorly, the ablation extended to about 1 cm above the callosomarginal



Fig. 14 Record of lesion in the right hemisphere of P-1.

sulcus, and inferiorly, to about the level of the tip of the central fissure.

N. ventralis posterolateralis was almost completely degenerated throughout. The posterior part of n. lateralis posterior showed retrograde changes in both thalami. The anterior part of n. pulvinaris lateralis was degenerated and a small dorsal portion of n. pulvinaris inferior. The lateral geniculate body showed degeneration in its medial portion throughout all layers for the whole length of the nucleus. No changes were observed in any other nuclei.

ANALYSIS OF TEST RESULTS IN RELATION TO LESIONS

The thalamic degeneration and the principal experimental results are summarized in table 9. Combined removal of the lateral surfaces of the temporal and posterior parietal lobes (the parieto-temporo-preoccipital region) was consistently followed by alterations of behavior only in visual discriminative learning, in patterned string problems, in a conditional reaction, and possibly in taste preference. Other deficits, not shown by all animals, were present in visual acuity and extent of the visual field, object recognition, tacto-kinesthetic abilities, auditory localization, and delayed reaction. No change was found in any animal in an auditory association problem, in food selection, or in general activity.

The temporal lobectomized animal showed deficit in visual discrimination learning, patterned string problems, conditional reaction, delayed reaction, and changes in taste preference, in food selection, and in tractability. There was also lack of retention of a roughness discrimination. No change appeared in visual acuity and extent of visual field, object recognition (except transiently), other somatosensory tests, or general activity. The parietal lobectomized animal showed deficit in roughness and weight discriminations, but none in tactile size and form discriminations, nor visual discriminations. Other tests were not made.

TABLE 9

Thalamic degeneration and experimental results

The extent of retrograde degeneration in selected thalamic nuclei is expressed by 0 (none), + (small), ++ (moderate), +++ (large). Deficit on the tests listed is indicated by 0 (none) or V (present). R and L, for thalamic degeneration, refer to the right and left hemispheres; for the tactile tests, they refer to the hand *contralateral* to the designated hemisphere.

THALAMIC DEGENERATION	PTO-1		PTO-2		PTO-3		PTO-4		T-1		P-1	
	R	L	R	L	R	L	R	L	R	L	R	L
VPL	0	0	0	0	0	0	0	0	0	0	+++	+++
LP	+++	+	+	+	+	+	0	+	0	0	+	+++
P	+++	+	+++	++	+++	++	+++	++	+	+	+++	++
LG	0	0	++	++	+	++	+	+	0	0	++	++
MG	+	+	+	+	++	++	+	++	+++	+++	0	0
Experimental results												
Visual	Primary visual capacities		0	V	V	0	0	0	0	0	0	0
	Object recognition		0	V	V	V	V	V	V	V	V	0
	Color habit		V	V	V	V	V	V	V	V	V	0
	Pattern habit		V	V	V	V	V	V	V	V	V	0
	Conditional reaction		V	..	V	V	V	V	V	V	V	..
	Delayed reaction		0	..	V	0	0	0	0	V	0	0
	Tactile	Size habit		0	0	0	V	V	V	V	0	0
Form habit		V	0	..	0	0	V	0	0	0	0	
Roughness habit		0	0	..	0	0	0	V	V	V	V	
Weight habit		0	0	0	V	V	V	V	V	

¹ Only one score is given for P-1, because he used either hand randomly during both pre- and postoperative training.

We shall attempt to integrate the anatomic and behavioral data with reference to the following questions:

1. Are the observed defects caused by loss in primary sensory capacities resulting from involvement of sensory areas or interruption of radiations?

2. Can the defects be ascribed to disruption of a thalamo-cortical system? Within the cortical region studied, is there a more restricted area, destruction of which is critical for the production of all or some of the symptoms?

Relation of symptoms to sensory losses

The site of the lesions involves risk of damage to the visual, auditory, and somesthetic sensory systems. Figure 2 shows the degeneration in the lateral geniculate nuclei for those animals in whom it could be established. Since in all these animals the only damage to the striate cortex was very slight and immediately adjacent to the lunate sulcus, it is probable that accidental partial interruption of the optic radiations is the cause of the degeneration. Demonstrated reductions in acuity and restrictions of the visual field are less than might be expected from the extent of nuclear degeneration. Only PTO-3 gave clear evidence of field defects (upper right quadrant), yet the nuclear degeneration indicates that he had a nearly complete right hemianopia together with a peripheral defect in the left ventral quadrant. In the other cases the degenerations indicate that some vision remained in each quadrant, and the field tests are inadequate to detect such smaller scotomata. The animals with the most extensive involvement of the caudal (macular) portion of the nucleus were PTO-2 and PTO-3. Both these animals gave evidence of reduced acuity.

These primary sensory defects, however, are not sufficient to account for the deficits in visual discriminative learning, in patterned string problems, and in the conditional reaction. In PTO-1 and T-1 the lateral geniculates were intact bilaterally, and in PTO-4 the degeneration was relatively slight and limited to peripheral parts, yet the latter three animals were also handicapped in the tests mentioned. Furthermore, P-1, despite

extensive bilateral degeneration in the lateral geniculate, involving the macular portion, readily learned the visual discrimination problems.

On the other hand, it may be significant that in our cases, a relatively permanent loss of the ability to recognize objects (as shown by failure to discriminate food from inedible objects) occurred only in those animals (PTO-2 and PTO-3) with deficits in acuity and greatest amount of degeneration in the lateral geniculates. That such degeneration is not, however, a sufficient condition for the appearance of this symptom is suggested by Lashley's cases ('48) with comparable degeneration in the macular portion of the geniculates and no failures of recognition.

Object agnosia has previously been said to follow temporal lobe lesions (Klüver and Bucy, '38). In the only case reported anatomically (Bucy and Klüver, '40), there was degeneration both in the lateral geniculate and in the posterior nuclear group. Our temporal lobectomized subject (T-1) did not fail to recognize food except for the few days immediately following operation. In this animal we found no degeneration in the lateral geniculate and only minimal degeneration in the medial pulvinar. Consequently it may be that concomitant damage to both the temporal neocortex and the geniculo-striate system is necessary to produce failures in object recognition. It is noteworthy that von Monakow ('14, pp. 481-488) expressed the view that permanent visual agnosia results only from a combination of damage to the visual cortex together with pathology in other cortical parts.

The symptom of spatial disorientation has been interpreted by Jacobsen ('36) as based upon "dissociation of visual and kinesthetic space." Lashley ('48), on the contrary, believes it more plausible to assume that primary visual defects, resulting from invasion of the optic radiations, are responsible. Only two of our animals (PTO-2 and PTO-3) were disoriented. Although these animals had field and acuity defects, it is probable from the anatomical results that P-1, who was not disoriented, had primary visual defects of comparable se-

verity. This result makes Lasbley's interpretation questionable. Our results are likewise suggestive with regard to Jacobsen's explanation. The fact that PTO-2 was among those minimally affected on the somesthetic tests indicates that kinesthetic disturbance played no significant part in his disorientation. Our findings suggest that disorientation in space is related to primary visual defects combined with disturbances of complex visual processes, rather than merely to primary visual disability or to simultaneous visual and kinesthetic defects.

Disorientation in visual space probably accounts for the absence of localization of sounds in PTO-2, our most severely disoriented animal. This alteration of behavior did not appear to be specifically an auditory deficit, for, excluding sound localization, both his native and acquired reactions to sound were unaffected. It is notable that all subjects in the parieto-temporo-preoccipital group and the temporal lobectomized animal had degeneration in the medial geniculate, which in some of the subjects was more extensive than that in PTO-2. None of them however, except PTO-2, showed deficit on any of our auditory tests.

With regard to somatosensory status, P-1 was the only animal in whom the relay nucleus (*n. ventralis posterolateralis*) included areas of degeneration. Yet all the subjects showed some deficits (except PTO-2, who was incompletely tested). Furthermore, the degree of decrement in P-1 was similar to that in PTO-3 and not as great as in PTO-4. Therefore, primary sensory impairment resulting from interruption of the ascending afferent pathways offers no reasonable explanation of the deficits found.

The possible alteration of taste preference, i.e., that relatively more of the bitter solution was accepted postoperatively in the three subjects, is also unrelated to primary sensory involvement, for none of our subjects showed any degeneration in *n. ventralis posteromedialis* (Patton, Ruch, and Walker, '44).

Thus, the question of whether the observed deficits necessarily resulted from primary sensory impairment can be answered in the negative. These disturbances can be produced without demonstrable changes in thalamic relay nuclei.

The role of "associative" thalamo-cortical systems

If involvement of the relay nuclei can be ruled out as a necessary condition for the production of deficit, can the observed symptoms be ascribed to interference with an "associative" thalamo-cortical system? What cortical areas appear to be especially concerned with the functions tested? Retrograde degeneration in thalamic nuclei was consistently found in all members of the parieto-temporo-preoccipital group only in n. pulvinaris lateralis and in the medial geniculate body. In the temporal lobectomized animal, however, there was no degeneration in any thalamic nucleus except the medial geniculate and a narrow strip of n. pulvinaris medialis. It is unreasonable to suppose that the common thalamic degeneration, i.e., that in the medial geniculate body, was involved in the production of the deficits which were common to both the parieto-temporo-preoccipital group and the temporal lobectomized animal. Therefore, these abnormalities cannot be ascribed to interference with a thalamo-cortical system, but rather to damage to the cortex itself. Since the deficits on the visual problems occurred after both the parieto-temporo-preoccipital and the temporal lobe excisions, but not after the parietal lobe removal, an obvious possibility is that the temporal neocortex, the area of overlap, is critically involved. This hypothesis was confirmed in a subsequent study (Chow, '50), in which visual deficits similar to the ones found in this study resulted from lesions confined within the lateral surface of the temporal lobe.

The significance of an "associative" thalamo-cortical system for tacto-kinesthetic discriminative abilities remains in doubt. Degeneration in n. lateralis posterior and in n. pulvinaris is present in the parieto-temporo-preoccipital group and in the parietal case, yet the degree of impairment in these

subjects was quite dissimilar. The extent and location of degeneration in these two nuclei varies widely after apparently similar cortical removals (note especially the two sides of PTO-1). Magnitude of degeneration is not clearly related to somesthetic deficit. A previous study (Blum, '50) indicated that extensions of parietal lesions into the posterior temporal lobe resulted in a greater somatosensory deficit than posterior parietal removals alone. Comparison of the results on P-1 with those of the hand contralateral to the larger lesion in PTO-4, where the major difference in the ablations was the inclusion of temporal neocortex in the latter, confirms the suggestion that the posterior temporal cortex participates in somesthetic discriminatory function. That this region is not focally concerned in this function, however, is shown by the slight effect of temporal lobectomy on somatosensory discrimination problems (T-1).

The traditional importance of the postcentral gyrus and superior parietal lobule in somatosensory discriminative capacity is not borne out by our findings. Of the two animals of the parieto-temporo-preoccipital group with most extensive involvement of the postcentral region (PTO-1 and PTO-4), the former was minimally affected, whereas the latter showed marked deficits; moreover, PTO-3, with less postcentral damage than PTO-1, was more severely handicapped. The results of Ruch and Fulton ('35) showed that the postcentral gyrus and superior parietal lobule are not the sole cortical locus of somatosensory processes. Our data further suggest that, for somesthetic discriminative learning, this region is not even a primary focus. It is true that inclusion of the postcentral gyrus in a parietal ablation causes more severe impairment of locomotor and manipulative capacities, but these increased disabilities are not reflected in correspondingly poorer performance on formal somatosensory discrimination tests.

The role of any thalamo-cortical system in mediation of more complex psychological function, such as the conditional reaction and delayed reaction tests presumably require, ap-

pears to be of little significance. Severe disturbance in a conditional reaction and in delayed reaction results from an operation which leaves the thalamus almost completely intact (temporal lobectomy in T-1). The result on the latter problem is complementary to that of Jacobsen and Walker (unpublished data, cited by Walker, '40) who found that direct damage to n. medialis dorsalis failed to produce the same incapacity on this test as that which results from prefrontal cortical lesions. The failure of T-1 on delayed reaction contrasts with Jacobsen's results on partial temporal lobectomized and other control cases ('36), which indicated strict localization in the frontal granular cortex.

In answer to our second question, therefore, the defects do not appear to be highly correlated with disruption of thalamo-cortical systems. For visual discriminative learning, there is a strong suggestion in our data that a critical focus exists in the temporal neocortex, an area receiving few or no thalamic projection fibers. In somesthesia, no cortical focus has as yet been demonstrated. The dependence of deficit on extent of degeneration in "associative" thalamic nuclei is questionable. Loss of more complex associations also seems to be attributable to removal of temporal cortex, without retrograde changes in "associative" thalamic nuclei.

DISCUSSION

It has been generally held that the cortex adjacent to each primary sensory projection area constitutes a specialized integrative or associative area for the corresponding sense modality. The present study contributes evidence against the traditional conception that the postcentral gyrus (exclusive of the projection field of n. ventralis posterior) and the pre-occipital region are of sole or prime importance to somatosensory and visual integrations, respectively. Not only does damage to the areas immediately adjacent to the sensory projection fields cause at most only slight and transient de-

ficits (Ruch and Fulton, '35; Lashley, '48), but lesions elsewhere which spare these areas may produce severe impairment. In vision, such a region probably exists within the temporal lobe. For somesthesia, this and other studies (Evans, '35; Ruch, Fulton and German, '38) have suggested that the posterior parietal lobule is probably of greater importance than the convexity of the postcentral gyrus. Somatosensory discriminative function appears to be widely represented in posterior association cortex, including temporal and preoccipital regions. These considerations suggest that there is no functional basis for postulation of wholly discrete visuospsychic and somatopsychic areas. (Our results in audition and gustation are not sufficiently conclusive to support extension of the conception to these senses.)

Additional data relevant to the problem of organization in the posterior association area is supplied by a consideration of the nature, or pattern, of the disturbances following the ablations we made. It is significant that our subjects did not show a general confusion or deterioration, such as would result from involvement of a general factor. Performance on the visual and somatosensory tests was not affected equally, and moreover, during the same period that some of the subjects were failing on the visual discrimination problems, they were succeeding on the somatosensory tests. At least for the parieto-temporo-preoccipital group, we can also say that there was no impairment of some general "intellectual" function, in so far as our two tests of ability to respond differentially according to context are valid measures of such capacity. If such a function had been disturbed, we should have expected a deficit on both these tests, whereas these animals showed impairment on only one.

The deficits in visual tasks were also obviously not mere amnesias or losses of specific engrammata. The animals required many more trials than preoperatively to reacquire the habits, although eventually all the subjects except PTO-2 relearned the color discrimination, and all except PTO-2 and

PTO-3, the pattern discrimination.⁴ The capacity for reacquiring such habits was impaired, but not totally lost. The fact that PTO-1 and PTO-4 relearned the pattern discrimination demonstrates that this cortical sector is not *essential* for an eventual high level of performance on such discriminations, but suggests rather that it exerts a facilitatory influence on the learning process.

That the deficits shown on the somesthetic problems were also not amnesias is indicated by the transfer of the discriminative reactions to the untrained hand after operation. In most cases, the animals who changed hand preference required fewer trials than preoperatively to relearn the problems. The different postoperative status of the two hands, e.g., where deficit was shown with the trained but not the untrained hand, suggests that the disturbance involved relative inaccessibility of the sensations received from the more severely impaired side to the discriminatory process, rather than amnesia for the learned habit.

The constellation of symptoms thus might be interpreted as a perceptual disorder without basis in general confusion, sensory defect, or loss of particular memories. Such perceptual function has generally been assigned to specialized "integrative" or "associative" areas, the organization of the brain being cast into a mold derived from an atomistic psychology. It is difficult, however, to subsume the results of ablation of the "associative" areas under such a rubric. Our data suggest that the basic disturbance is not most aptly characterized as one of integration of sensations. Discriminations such as those of colors or weights, in which the necessity of integration of sensations appears *a priori* to be

⁴Although it may seem significant that the irrecoverable losses of the discrimination habits occurred only in those animals with extensive degeneration in the macular portion of the geniculate, the ready learning of these habits by P-1 (who had similar bilateral degeneration in the geniculate) rule out such degeneration as the sole explanation of the "permanent" symptoms. It is possible that an explanation similar to the one we have proposed for object agnosia and spatial disorientation applies here.

minimal, are as much affected as more complex ones involving cues derived from forms or patterns.

A clue to the level at which disturbance exists is furnished by the performance on the somesthetic discrimination problems of the animals who changed hand preference postoperatively. The fact that they were in most cases able to relearn with the untrained hand in a smaller number of trials than originally taken indicates that the learned discriminative reaction was not lost. Moreover, this transfer from hand to hand demonstrates that the habit was not separately organized for each hand. The defective performance with the trained hand cannot, therefore, be ascribed to ablation of a separate center for organization of sensations from that member. Rather, it appears probable that the disturbance is at a high level of the receptive chain, such that the afferent impulses, although still entering into the thalamo-cortical arcs which are concerned in so-called primary or simple sensation, are no longer so readily available to cortico-cortical circuits capable of mediating the modes of perception which certain forms of discriminative behavior require. We may speculate as to the reason for this decrease in availability of the incoming impulses to higher-order circuits. To activate these circuits readily, possibly a tonic substrate of facilitatory impulses is required to join with the afferent excitations from the primary sensory areas.

The present study suggests that the parieto-temporo-preoccipital cortex includes a number of foci of prime importance in facilitating discriminative learning and also presumably "higher" mental abilities. For both the processes mediating discriminative reactions and for the capacities demanded by more complex problems, analogous anatomic bases appear to exist within associative cortex, i.e., areas of maximal significance for each, together with less highly involved peripheral regions. The evidence strongly suggests that these foci are not coincident, with the qualification that the total regions concerned in the various capacities probably overlap. These peripheral regions appear to be capable of participat-

ing in qualitatively different functions. It is possible that they form common neuronal pools which can be reciprocally activated in the service of one function at one time and a different one at another.

SUMMARY

1. Extensive cortical ablations in the parieto-temporo-preoccipital region were made in 4 monkeys (*Macaca mulatta*); the temporal lobe was excised in a 5th monkey and the parietal lobe in a 6th.

2. Tests and observations of sensory perception in vision, somesthesia, audition, and gustation; of ability to respond differentially according to context; and of activity and temperament were made both pre- and postoperatively.

3. The parieto-temporo-preoccipital ablations were consistently followed by changes of behavior only in visual discriminative learning, in patterned string problems, in a conditional reaction, and possibly in taste preference. Other deficits, not shown by all animals, were present in visual acuity and extent of the visual field, object recognition, tacto-kinesthetic abilities, auditory localization, and delayed reaction. In three of these animals, there was postoperative transfer of somesthetic discriminative reactions from the trained to the untrained hand, yet subsequent inferior performance with the preoperatively trained hand. No change was found in any animal in an auditory association problem, in food selection, or general activity.

4. The temporal lobectomized animal showed deficit in visual discriminative learning, patterned string problems, conditional reaction, and delayed reaction, and changes in taste preference, in food selection, and in tractability. There was also lack of retention of a roughness discrimination. No change appeared in visual acuity and extent of visual field, object recognition (except transiently), other somatosensory tests, or general activity.

5. The parietal lobectomized animal showed deficit in roughness and weight discriminations, but none in tactile size

and form discriminations, nor visual discriminations. Other tests were not made.

6. After completion of tests, the animals were sacrificed and the cortex and thalamus reconstructed from serial sections.

7. The test results are analyzed with reference to the locus and extent of cortical lesion and thalamic degeneration. (a) Interruption of relay thalamo-cortical circuits is not essential to the production of deficits in visual and somesthetic discriminative learning, in conditional reaction, or delayed reaction. (b) Deficits in visual discriminative learning, in conditional reaction, and delayed reaction can be produced with minimal damage to "associative" thalamo-cortical systems. In somesthetic discriminative learning, the importance of such systems is questionable.

8. Thus, the observed deficits cannot be ascribed to primary sensory impairment. Analysis of the test results further show that these defects resulted neither from general deterioration nor from losses of specific engrammata.

9. On the basis of the results, it is proposed that the parieto-temporo-preoccipital region, exclusive of sensory projection areas, contains separate foci, concerned with facilitating discriminative learning in vision and somesthesia, and also acquisition of more complex habits; within this sector, it appears probable that there are also common neuronal pools which are capable of participation in a variety of functions.

LITERATURE CITED

- BLUM, J. S. 1950 Cortical organization in somesthesia. *Comp. Psychol. Monogr.* (In press.)
- BONIN, G. VON 1941 A preliminary study of the brain of man, chimpanzee and maeaque. *J. Comp. Neur.*, 75: 287-314.
- BUCKY, P. C., AND H. KLÜVER 1940 Anatomic changes secondary to temporal lobectomy. *Arch. Neur. Psychiat.*, 44: 1142-1146.
- CHOW, K. L. 1950 Effect of partial extirpations of posterior association cortex on visually mediated behavior in monkeys. *Comp. Psychol. Monogr.* (In press.)

- EVANS, J. P. 1935 A study of the sensory defects resulting from excision of cerebral substance in humans. *Proc. Assn. Res. Nerv. Ment. Dis.*, 15: 331-370.
- FULTON, J. F. 1943 *Physiology of the nervous system*. New York, Oxford University Press, ix + 614 pp.
- HALSTEAD, W. C. 1947 *Brain and intelligence*. Chicago, University of Chicago Press, xiii + 206 pp.
- JACOBSEN, C. F. 1936 The functions of the frontal association areas in monkeys. *Comp. Psychol. Monogr.*, 13: 1-60.
- KLÜVER, H., AND P. C. BUCY 1938 An analysis of certain effects of bilateral temporal lobectomy in the rhesus monkey, with special reference of "psychic blindness." *J. of Psychol.*, 5: 33-54.
- LASHLEY, K. S. 1948 The mechanism of vision: XVIII. Effects of destroying the visual "associative areas" of the monkey. *Genet. Psychol. Monogr.*, 37: 107-166.
- LASHLEY, K. S., AND G. CLARK 1946 The cytoarchitecture of the cerebral cortex of Ateles: a critical examination of architectonic studies. *J. Comp. Neur.*, 85: 223-305.
- MONAKOW, C. VON 1914 *Die Lokalisation im Grosshirn*. Wiesbaden, Bergmann, xii + 1033 pp.
- PATTON, H. D., AND T. C. RUCH 1944 Preference thresholds for quinine hydrochloride in chimpanzee, monkey, and rat. *J. Comp. Psychol.*, 37: 35-49.
- PATTON, H. D., T. C. RUCH, AND A. E. WALKER 1944 Experimental hypogeusia from Horsley-Clarke lesions of the thalamus in *Macaca mulatta*. *J. Neurophysiol.*, 7: 171-184.
- RUCH, T. C., J. F. FULTON AND W. J. GERMAN 1938 Sensory discrimination in monkey, chimpanzee, and man after lesions of the parietal lobe. *Arch. Neur. Psychiat.*, 39: 919-937.
- WALKER, A. E. 1940 The medial thalamic nucleus. *J. Comp. Neur.*, 73: 87-115

In all three animals who shifted handedness, there was evidence of spontaneous habit transfer from the trained to the untrained hand (on all problems in PTO-1, and on two of the four problems in PTO-3 and PTO-4).

C. Auditory tests.

Startle: The startle reaction to a loud sound was not affected in any animal by the operations. P-1 was not tested.

Localization: P-1 was not tested on this problem. All animals retained the ability to localize loud sounds, except PTO-2.

Auditory association: PTO-2 and P-1 were not trained. All other animals showed almost perfect retention of this association in the postoperative tests.

D. Gustatory tests.

Taste preference: (fig. 1). Only three animals, PTO-1, PTO-3, and T-1, were tested. At the quinine concentrations used, all three animals were preoperatively within the normal ranges, as established by Patton and Ruch ('44), for proportion of the bitter solution accepted in total fluid intake. Postoperatively, PTO-1 was outside the normal range at the lowest concentration. PTO-3 and T-1 accepted slightly more of the bitter solution than preoperatively at all or most concentrations, and were outside the normal ranges at the two highest concentrations.

Food selection: P-1 was not tested. Of the others, the only animal who showed an alteration in food habits following operation was T-1, who ate meat and fish avidly for the first postoperative month, less enthusiastically for another two months, and finally refused to accept them.

II. Tests of ability to respond differentially according to context.

Conditional reaction: (table 7). PTO-2 and P-1 were not tested. The results for condition A have already been given

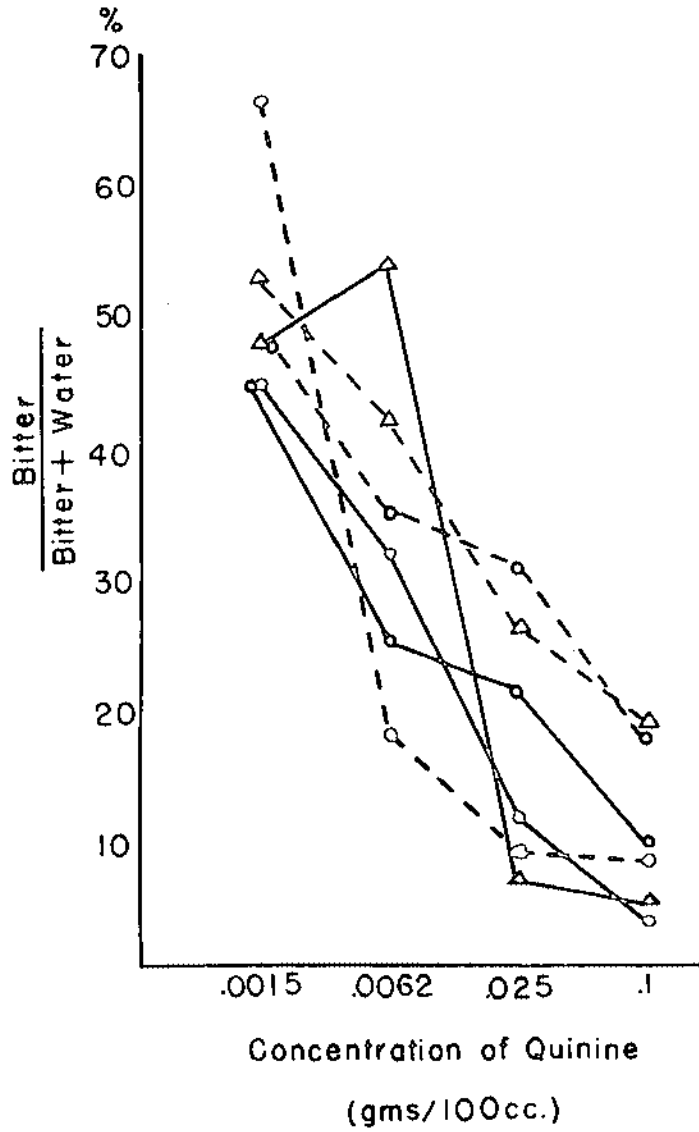


Fig. 1 Taste preference curves for PTO-1 (filled circles), PTO-3 (hollow circles), and T-1 (triangles). The solid lines represent preoperative consumption; the interrupted lines, postoperative consumption.

under "Color discrimination." All animals required more trials than preoperatively to relearn condition B (reversal of preference established in condition A). All animals lost the habit of responding according to the conditional cue, and all of the PTO group required more trials to relearn it than originally. PTO-1 and PTO-4 were only slightly retarded, but PTO-3 took about 4 times the number of preoperative trials. T-1 failed completely within the limits of training.

TABLE 7
Conditional reaction

Trials, errors and reversals required to reach a criterion of 4 consecutive immediate reversals, determined by the conditional cue, with no more than one error in the subsequent 9 trials following reversal

SUBJECT NO.	PREOPERATIVE			POSTOPERATIVE		
	Trials	Errors	Reversals	Trials	Errors	Reversals
PTO-1	438	147	16	543	150	20
PTO-2
PTO-3	194	97	8	819	298	18
PTO-4	206	51	12	275	60	13
T-1	601	194	10	(1039) failed	(453)	(3)
P-1

Delayed reaction: (table 8). PTO-2 was not tested postoperatively, and P-1 was not tested preoperatively. The other animals of the PTO group did not lose the ability to do this problem; in fact, PTO-1 and PTO-4 required fewer trials to meet the criteria than preoperatively. In the case of PTO-3, however, there was apparently increased difficulty after operation when a screen hid the food cans during the delay interval. T-1 failed within 500 trials to meet the criterion at 15 seconds without the screen, and also failed in an additional 500 trials at 5 seconds with the screen. The postoperative scores for the initial experience of P-1 with this problem ap-

pear much worse than those of any of our normals. However, in a subsequent series of normal animals (cf., Chow, '50), similar poor scores were obtained.

III. Observations of activity and temperament.

Only insignificant changes in the level of general activity were seen postoperatively. The activity of P-1 was not recorded, but he did not appear to be more or less active than preoperatively.

TABLE 8

Delayed reaction

Total trials and errors required to reach a criterion of 90% correct within a 30-trial session at 5, 10, and 15 seconds delay both with and without interposition of an opaque screen during the delay interval

SUBJECT NO.	PREOPERATIVE		POSTOPERATIVE	
	Trials	Errors	Trials	Errors
PTO-1	680	128	270	22
PTO-2 ¹	540	92
PTO-3	530	103	630	165
PTO-4	1020	174	540	90
T-1	330	32	(1090)	(352)
P-1 ¹	1430	339

¹ Subject P-1 was not tested preoperatively; subject PTO-2, not postoperatively.

None of the animals except T-1 and PTO-2 showed any detectable changes in temperament. T-1 became much more tractable and less fearful. She permitted herself to be picked up and handled, even by strangers, and could hardly be prevented from clinging to the experimenter. However, no behavior which could be interpreted as specifically hypersexual, such as has been reported in other monkeys with temporal lobectomies (Klüver and Bucy, '38), was observed, possibly because of her immaturity. PTO-2 reacted in a trance-like manner, with erection and pseudo-catatonic malleability, to petting. This condition began after the first operation and persisted until his death.

ANATOMIC DATA

Parieto-temporo-preoccipital lesions

The lesions in all the animals of the PTO series included the entire lateral surfaces of the posterior parietal and temporal regions, extending for variable distances on the inferior surface of the temporal lobe. The allocortical structures were

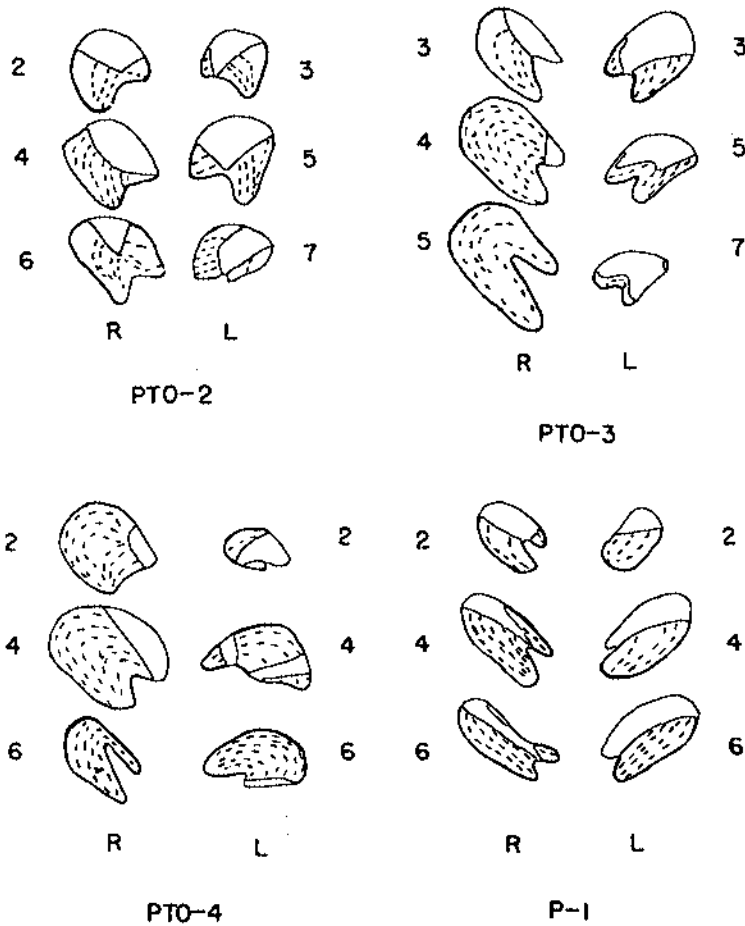


Fig. 2 Extent and location of degeneration (indicated in black) in the lateral geniculate bodies of the 4 animals in whom those nuclei showed retrograde changes. Section numbers indicate the serial order from anterior to posterior.

spared or only slightly damaged. The posterior extent of the lesion reached the lunate sulcus along its entire course in all cases, and the anterior extent, the intraparietal sulcus. Superiorly, the lesions extended to about 1 cm above the callosomarginal sulcus. The depths of the sulci were in general incompletely destroyed. The precise boundaries of the lesion differed somewhat among the various animals. Figures 3 to 10 show reconstructions of the cortical lesions, cross sections through the lesion, and retrograde thalamic degeneration.

Subsequent to completion of postoperative tests, ablations of prefrontal granular cortex were made in PTO-3 and PTO-4. Description of these lesions and of the thalamic degeneration presumed to have resulted therefrom will be reported elsewhere.

In the thalamus retrograde degeneration was consistently found in all cases only in *n. pulvinaris lateralis* and in the medial geniculate body. However, the position and extent of the degeneration within these nuclei varied, as indicated in the plates. No degeneration was found in any monkey in *n. ventralis posterior* or in *n. lateralis dorsalis*. (The degeneration in *n. medialis dorsalis*, the anterior group of nuclei, and *n. ventralis lateralis* in the thalami of PTO-3 and PTO-4 is presumed to have resulted from the subsequent frontal ablation.) There was bilateral degeneration of variable location and extent in the lateral geniculate bodies of all monkeys

Fig. 3 Record of lesion in PTO-1. In this and the following reconstructions of the cortical surface, complete excision is indicated by hatching and partial destruction by stippling. Preservation of the depths of sulci is indicated by interrupted lines. The position of the cross sections through the lesion are shown by the numbered lines on the surface drawings. In these cross sections the cortex is represented in black. Sections through the thalamus, from anterior to posterior, are shown below. Completely degenerated regions are hatched; regions of "doubtful" degeneration are stippled. MD, *n. medialis dorsalis*; VPL, *n. ventralis posterolateralis*; VPM, *n. ventralis posteromedialis*; LP, *n. lateralis posterior*; CM, *n. centrum medianum*; PL, *n. pulvinaris lateralis*; PM, *n. pulvinaris medialis*; PI, *n. pulvinaris inferior*; LG, lateral geniculate body; MG, medial geniculate body.

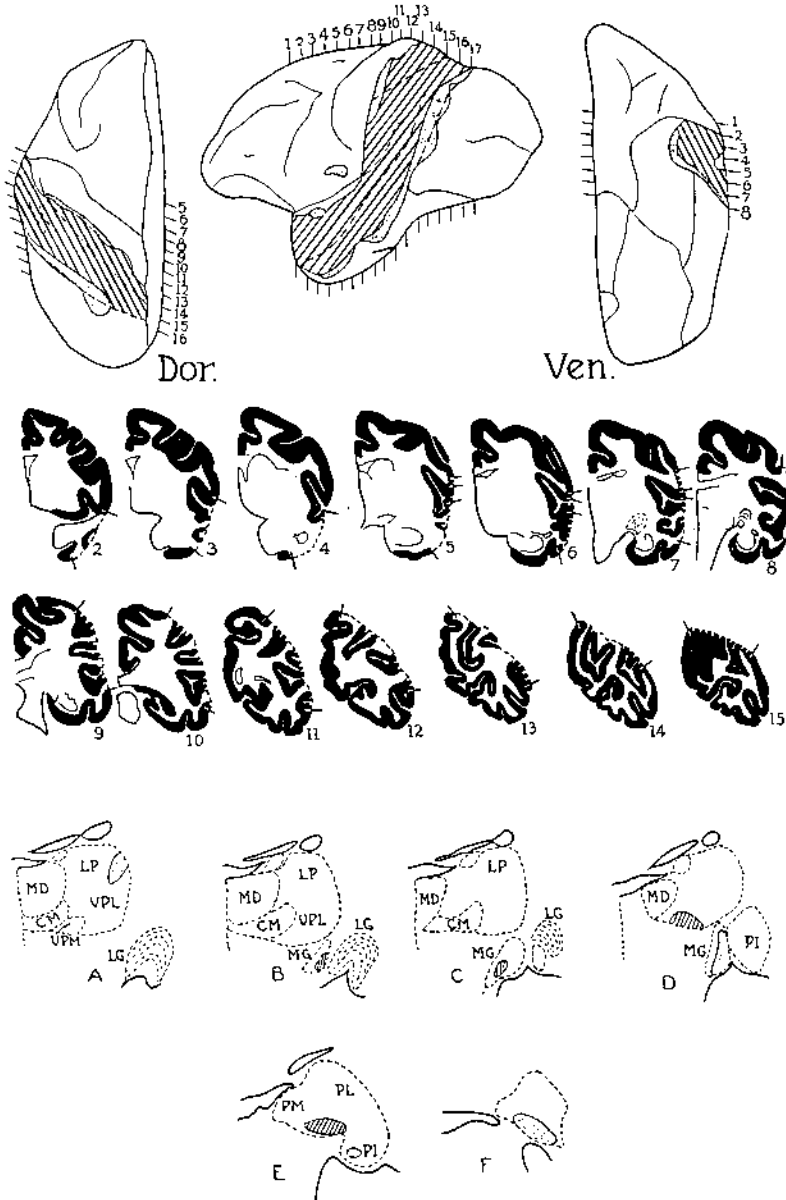


Figure 3

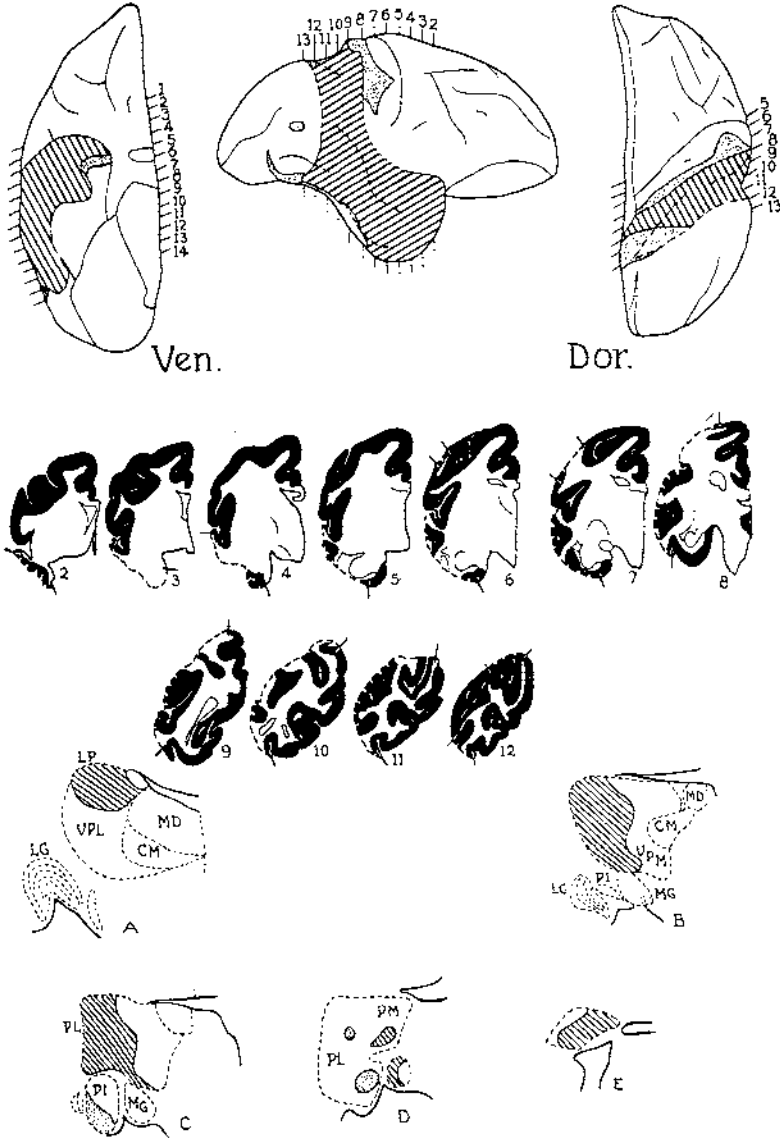


Fig. 4 Record of lesion in the right hemisphere of PTO-1.

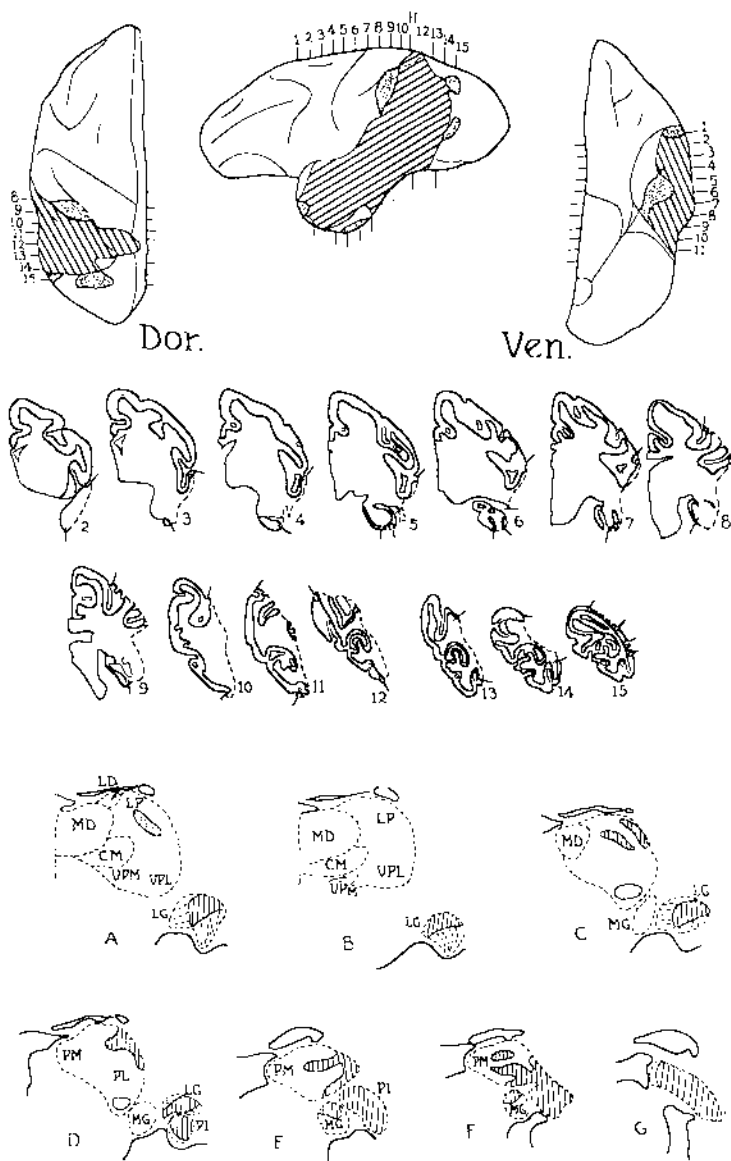


Fig. 5 Record of lesion in the left hemisphere of PTO-2.

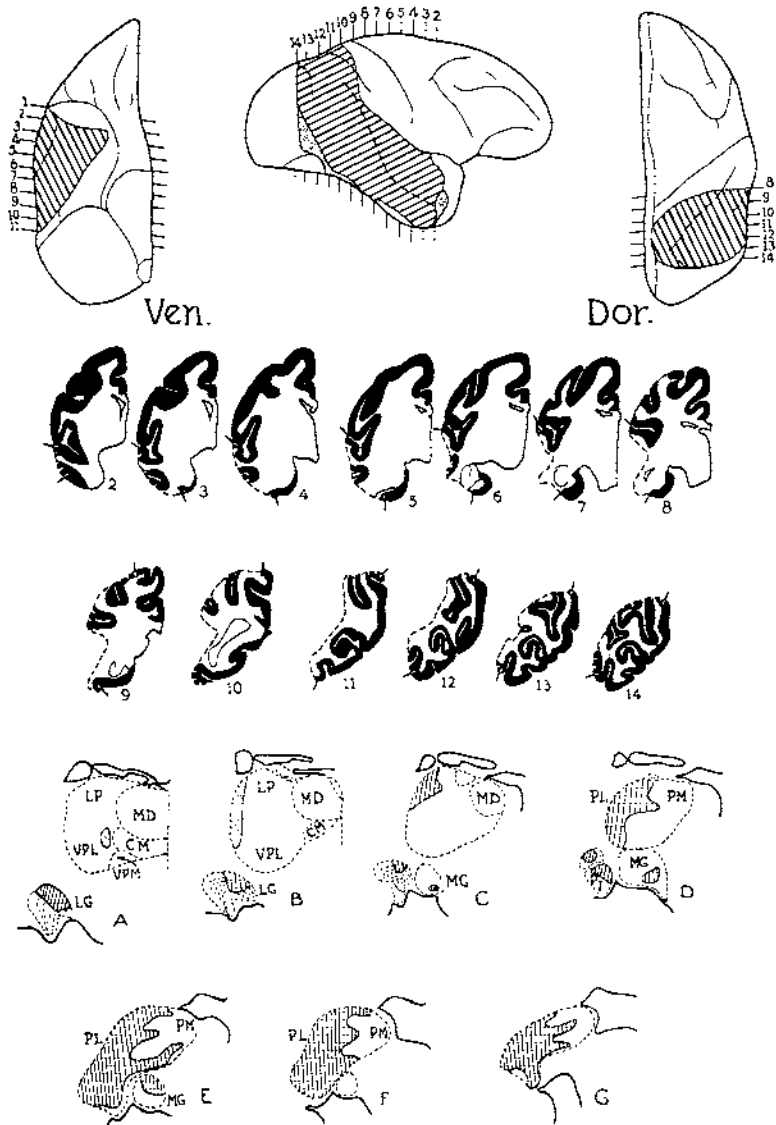


Fig. 6 Record of lesion in the right hemisphere of PTO-2.

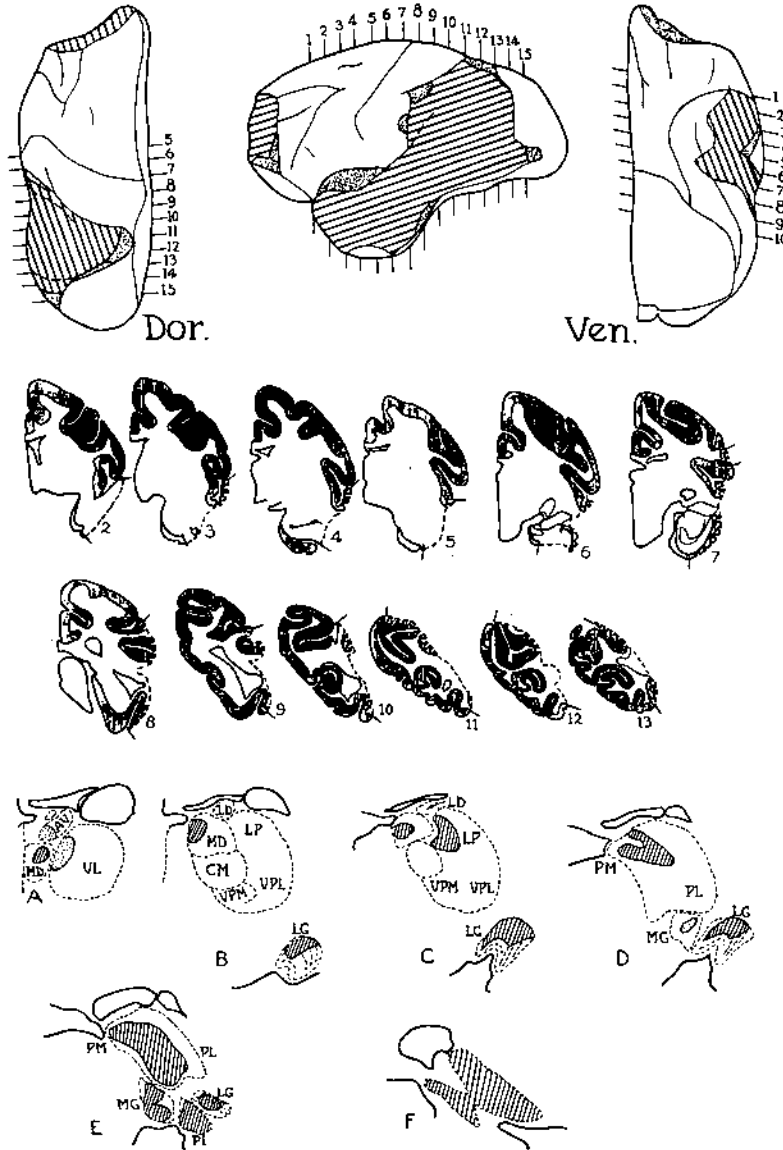


Fig. 7 Record of lesion in the left hemisphere of PTO-3.

(Reexamination of the thalamus shows that degeneration noted in nucleus L.P. in drawing C should be recorded as "doubtful" rather than "definite.")

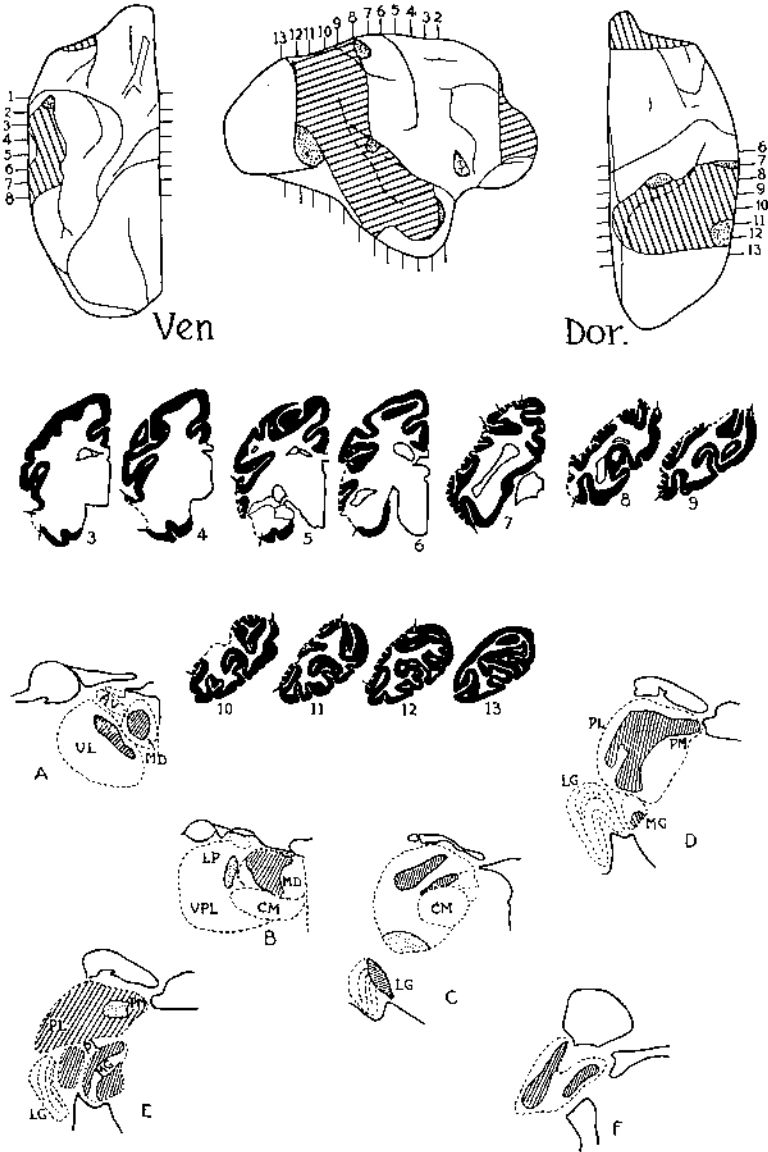


Fig. 8 Record of lesion in the right hemisphere of PTO-3.

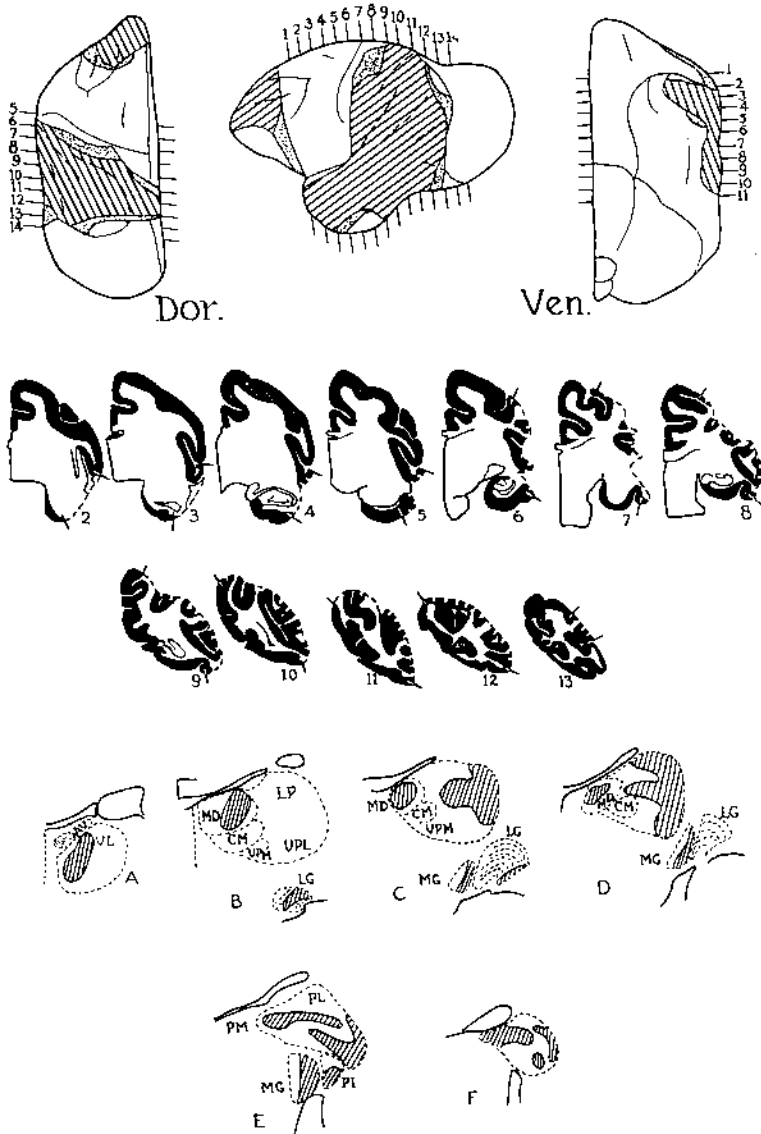


Fig. 9 Record of lesion in the left hemisphere of PTO-4.

(fig. 2), except in PTO-1 and T-1, where this nucleus was intact on both sides.

Temporal lesions: In T-1 (figs. 11 and 12), the temporal lobes anterior to the vein of Labbé, including allocortical

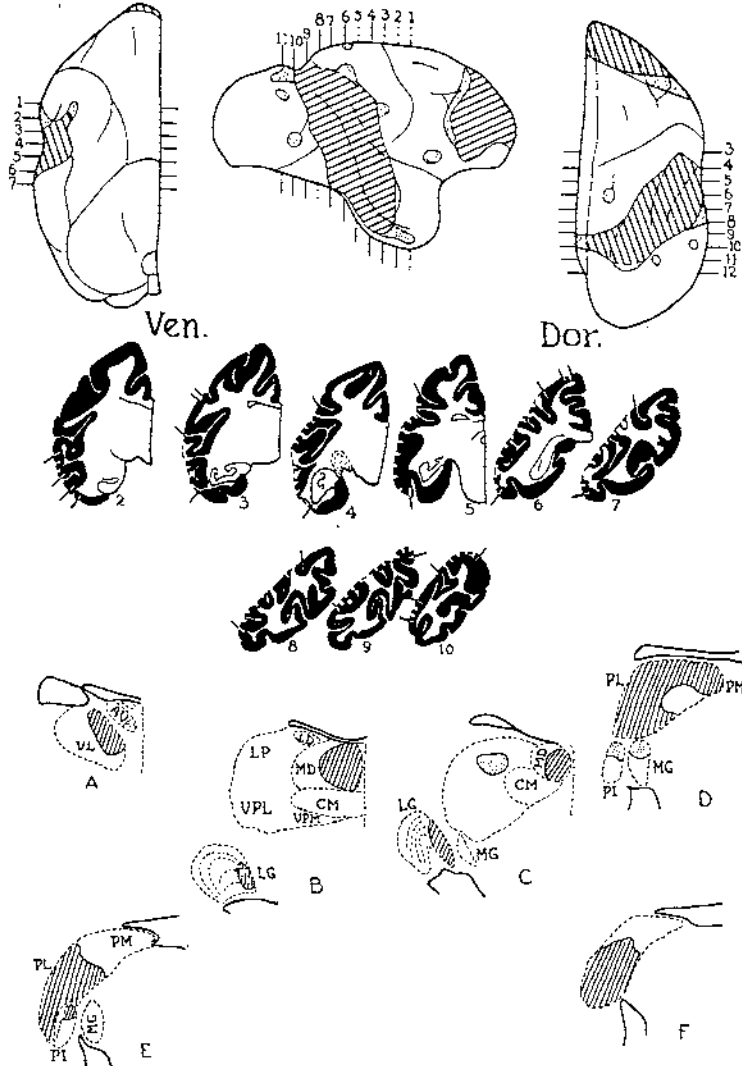


Fig. 10 Record of lesion in the right hemisphere of PTO-4.

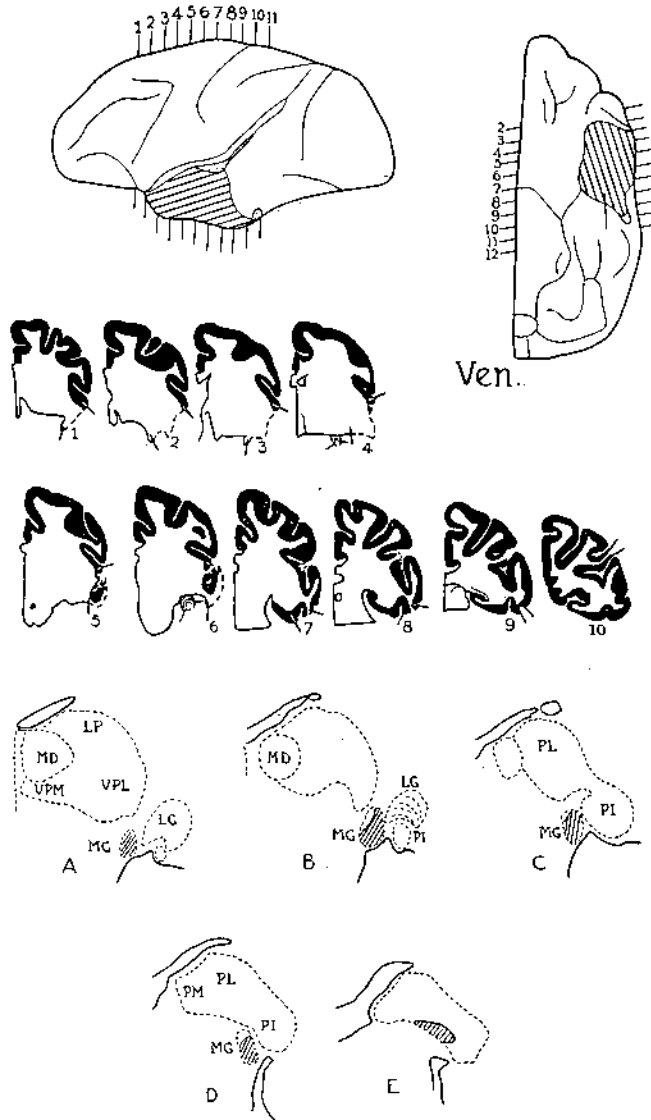


Fig. 11 Record of lesion in the left hemisphere of T-1.

structures, were excised, except for a small portion of the posterior part of the hippocampi. In addition, almost the entire superior temporal gyrus was removed.

The medial geniculate was almost entirely degenerated bilaterally. There was no degeneration in any other thalamic

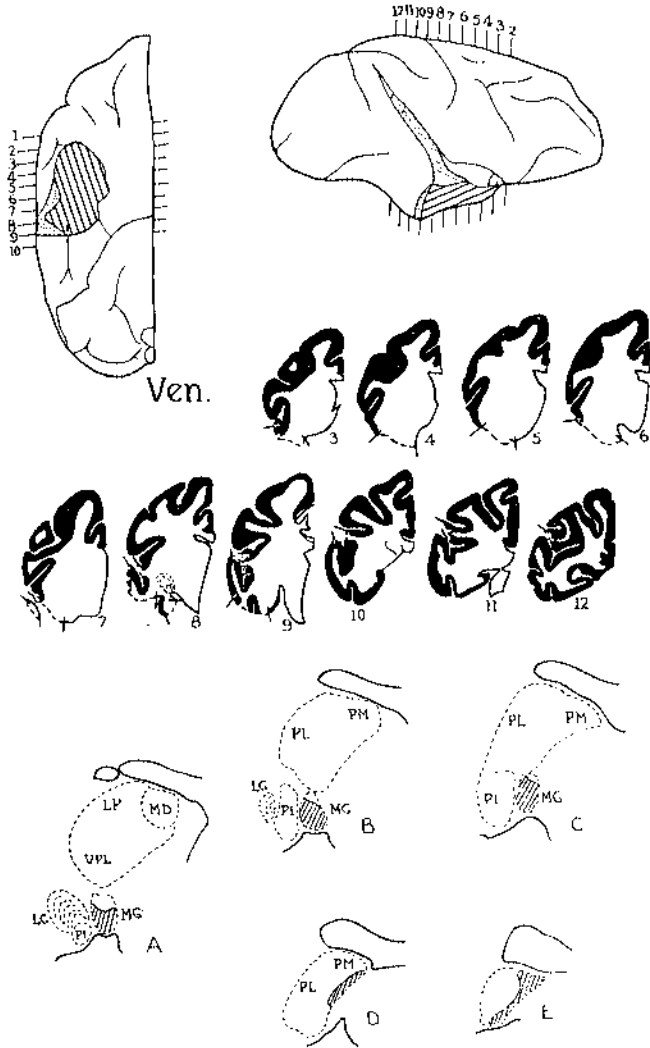


Fig. 12 Record of lesion in the right hemisphere of T-1.