The relative amounts of practice required by operated and by normal animals are shown by the following figures:

	Maze III	Maze II	Maze I
Normal animals:			
Errors in learning	47.4	16.2	7.3
Ratio on Maze I	6.5	2.2	1.0
Operated animals:			
Errors in learning	460.0	77.8	22.3
Ratio on Maze I	20.62	3.49	1.0
Ratio of operated on normal	9.7:1	4.8:1	3.0:1

These figures show clearly that the relative difficulty of the complicated mazes is greater for the animals with brain lesions than for normals. Whereas the operated animals required only three times as much practice for learning Maze II as did normals, they required almost five times as much for Maze III. This shows that the greater the difficulty of the maze for normal animals, the greater is the relative amount of retardation produced by brain injury.

For normal animals an increase in the number of culs-de-sac to be learned did not proportionately increase the difficulty of the problem. For the operated animals, on the contrary, increase in the number of culs-de-sac resulted in a disproportionate increase in the difficulty of the problem. This corresponds to the finding of Müller (1911) that, whereas learning by the "whole" method is advantageous for normal children, it is decidedly disadvantageous for the feeble-minded.

We must next inquire the relation of the three variables: extent of injury, complexity of the problem, and degree of retardation in learning. Is the relative increase in difficulty with complexity the same for all amounts of injury? To test this, the animals have been divided into groups by successive increments of 10 per cent destruction, and the average errors in learning the mazes computed for each group. These averages are given in Table XI. The groups are small, ranging from 4 to 11 cases, so that a good bit of chance variation is to be expected. With only two exceptions the increase in amount of practice for all mazes follows the increments in amount of destruction.

The ratios of practice required for Mazes II and III and IV

to that for Maze I are included in the table. The relative difficulty of Maze II in comparison with Maze I shows little change with increase in the extent of lesion. The records for Maze III, on the contrary, show a definite trend toward a disproportionate difficulty for the cases with greater injuries. This difference between the ratios for Mazes II and III is probably due to the fact pointed out before, that Maze II is more nearly equal in difficulty to Maze I than is indicated by the error records.

TABLE XI

COMPARISON OF THE RETARDATION IN LEARNING MAZES OF DIFFERENT COMPLEXITY PRODUCED BY LESIONS OF DIFFERENT MAGNITUDES

No. of Cases	Percentage of Destruction	Errors in Learning				Ratio to Maze I			
		Maze I	Maze II	Maze III	Maze IV	Maze I	Maze II	Maze III	Maze IV
8	1–10	6.6	15.4	33.4	72.0	1	2.3	5.0	10.9
4	11–20	7.2	40.0	33.7	266.0	1	5.5	4.7	36.9
11	21–30	31.8	43.5	46.2	396.0	1	1.3	1.4	12.4
4	31–40	29.3	63.2	53.0	485.0	1	2.2	1.8	16.5
4	41–50	34.7	52.8	53.0	580.0	1	1.6	1.8	17.0
7	50+	40.0	66.6	60.0	1,446.0	1	1.6	1.5	36.2

It may be noted in Table XI that for each of the mazes there is one short range in extent of lesion with marked increase in the amount of practice required for learning. For Maze I this increase is at 20 per cent (7.2 to 31.8 errors). For Mazes II and III it is at 10 per cent (15.4 to 40.0 and 72.0 to 266.0 errors). Whether this indicates a critical amount of destruction necessary to retard learning or is a chance variation cannot be determined from the data at hand. In the records for Maze IV there is no sharp break in continuity, so that it seems likely that it is a chance effort in the other records.

The data of Table XI with the irregularities smoothed out have been embodied in the graph of Figure 17. Amount of destruction, practice for learning, and relative difficulty of the problems for normals are illustrated as variables in the three dimensions. The absolute values are uncertain, but I believe that the figure represents a justifiable interpretation of the trend of the results.

ferences within a group of animals having extensive injuries to the cerebrum.

There are serious objections to the foregoing methods of measuring the reliability of tests. The use of intercorrelations of the results of training upon different problems involves the assumption that learning ability is a unitary function which should be revealed by any reliable measure—an assumption which is totally unjustified by the experimental literature on human or animal learning. The lack of a correlation between two reliable but dissimilar learning problems forms a valid objection to any conclusion concerning learning capacity in general, but it does not necessarily give an index of the adequacy of the measures to reveal individual differences in ability to learn either problem.

Failure to find a high correlation between the data on the first 10 trials of training and some arbitrary measure of complete learning is also not a conclusive argument against the validity of the latter, since a correlation between a reliable and an entirely unreliable measure need not be higher than between two unreliable ones. Where there is no other variable which can be measured more reliably, we cannot choose between different parts of the learning curve and must discard all measures as untrustworthy. But where some additional and measurable variable is introduced, it is possible to evaluate the measures of learning by their closeness of correspondence to this variable, provided it is not of such a character as directly to affect the measures themselves.

Thus a comparison of the extent of injuries within the occipital areas of the rat with the amount of practice required for relearning the habit of brightness discrimination revealed correlations of the order 0.72 by several criteria of learning and by all methods of subdividing the data which did not result in reduction of the range of variation. This shows that the retention tests were a fairly valid measure of the amount of brain injury, whether or not they actually measured retention.

In the present experiments, Table XI (page 73) shows the relation between the extent of brain injury and the rate of initial learning of four different mazes. The table includes five sets of

permutations, each of six figures. Among these thirty elements of the permutations there are only two inversions of the order from least to greatest. The probability of such a correspondence occurring by chance is less than one to fifty billions.

These considerations seem to me to form a valid argument against the extension of conclusions concerning the reliability of the maze, based upon studies of normal animals only, to any experiments in which other variables are introduced. Thus, although the scores made in the initial stages of practice do not correlate highly with the final measures of learning,[1] the consistency of the results and the closeness of correspondence between the records for final learning and the extent of brain injury indicate that, for the conditions of the experiment, Maze III and the Yerkes discrimination box provide an adequate measure of some function which is affected by brain injuries. They give no indication of the fineness of this measure, but this is a common defect of all methods of evaluating tests.

Whether we are dealing with learning ability in general, with a learning capacity specific for the problems in which the animals were trained, or with some other function than that of learning is not revealed by the correlation alone. It must be decided on the basis of other data; intercorrelations between results with different problems, analysis of the behavior essential for the performance of the habits, and the like.

DIFFICULTIES OF INTERPRETATION IN STUDIES OF BRAIN INJURIES

In analysis of the symptoms of brain injury it seems that we must take into account a number of variables which, because of practical difficulties of technique, are almost impossible of independent control. They enormously complicate the problem; yet, until we have some means of evaluating them severally, we

[1] I am not inclined to use any criterion of maze learning which does not involve the attainment of a fairly stable errorless performance. Our interest is primarily in the acquisition of the maze pattern, and only errorless trials give certain evidence for this. Improvement in time or reduction in errors may indicate that the pattern is being learned but in the earlier stages of training is probably indicative of nothing more than adaptation to a strange situation.

can form no true conception of the cerebral mechanisms. The variables which may be clearly recognized in a series of cases seem to be:

1. *Individual variation in localization.*—Anatomical studies of the area striata have shown that the cortical fields delimited by cell structure vary considerably from one individual to another. Adequate data of this sort are available only for this area, and even here give only the fact of variation without determination of the limits of the range or the distribution of variates. By physiological methods also, indication of this variability is obtained. Observations here are unambiguous only for the motor area, but the results of Franz (1915) show clearly that even in the two hemispheres of the same animal the arrangement of excitable points differs greatly. Whether this variability is primarily the result of anatomical differences or whether it indicates that functional organization is in some measure independent of structure is uncertain. My observations on temporal variation in the function of the motor area (Lashley, 1923) suggest that both anatomical variation and changes in physiological organization may be effective agents in producing the appearance of functional variability.

2. *Specific shock or diaschisis effects.*—Monakow (1914) has emphasized the rôle played in the production of recoverable symptoms by temporary loss of function in one center as a result of destruction of another. The conception is doubtless a valuable one for the understanding of many cases of spontaneous recovery, but its practical application is complicated by the frequent difficulty in distinguishing between spontaneous recovery and recovery as a result of re-education. We have as yet no understanding of the manner in which the diaschisis effect is produced or any way of predicting the most probable shock effects from injury to any particular locus.

3. *Vicarious function.*—Improvement through re-education has been interpreted as the assumption of the functions of injured parts by others which have escaped injury. There is much incorrect speculation in the older literature concerning the parts functioning vicariously, as the assumption that the precentral

gyrus of one side can assume the functions of that of the other; but there is no certain evidence that the reacquired functions are carried out vicariously by any specific loci. Attempts to discover such loci have been in almost all cases fruitless (Lashley, 1922) and point rather to a reorganization of the entire neural mass than to an action of specific areas. The spontaneous and re-educative improvements after cerebral lesions make it exceedingly difficult to draw final conclusions from any syndrome concerning cerebral function, since a gradual improvement may be ascribed to recovery from shock, even though it occurs during a post-operative retraining.

4. *Equipotentiality of parts.*—The term "equipotentiality" I have used to designate the apparent capacity of any intact part of a functional area to carry out, with or without reduction in efficiency, the functions which are lost by destruction of the whole. This capacity varies from one area to another and with the character of the functions involved. It probably holds only for the association areas and for functions more complex than simple sensitivity or motor co-ordination.

5. *Mass function.*—I have already given evidence (1927), which is augmented in the present study, that the equipotentiality is not absolute but is subject to a law of mass action whereby the efficiency of performance of an entire complex function may be reduced in proportion to the extent of brain injury within an area whose parts are not more specialized for one component of the function than for another.

6. *Disturbances of the equilibrium within functional systems.*—There is a considerable mass of evidence which suggests that some symptoms, particularly in the class of motor inco-ordinations, may result from disturbances in the functional equilibrium between centers, although no tissue essential to the performance of the disturbed activities is directly involved in the lesion. Thus unilateral lesions to the corpus striatum or to the cerebellum may produce marked disturbances of co-ordination although bilaterally symmetrical lesions involving the same structures produce but slight effects.

In evaluating any symptoms following cerebral lesion we must consider the possible intervention of each of these factors. In some cases the differentiation is relatively easy, as in ruling out diaschisis as an element in the production of a permanent defect of learning ability, but this is rather an exceptional instance. Wherever possible, I have attempted to distinguish the rôle of such different factors, but in many cases this must await the accumulation of far more evidence.

CHAPTER III

THE INFLUENCE OF CEREBRAL LESIONS UPON THE CAPACITY TO LEARN

In 1918 I reported a first attempt to determine the influence of the extent of lesions to the cerebrum upon the rat's ability to form a motor habit. For the purpose the double-platform box was used (Fig. 1). This is a problem box provided with a door
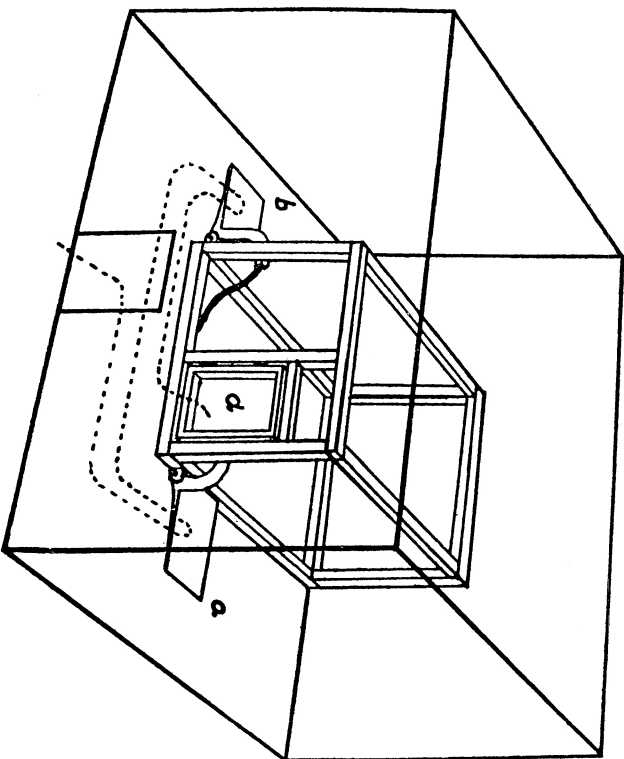

Fig. 1.—The double-platform box used in earlier studies. The door (d) is opened when the platforms (a, b) are successively pressed down.

which is opened by successively pressing down in predetermined order two platforms attached to opposite sides of the box. Nineteen animals were trained in this habit after cerebral lesions involving from 14 to 50 per cent of the cortex. The average amount of destruction was 28.4 per cent. The operated animals required only 75 per cent as much practice as normal animals learning

under the same conditions. Correction for the effects of motor disturbance in the operated cases indicated that the cerebral destruction produced no significant effect upon the learning ability for this habit. The rank-order correlation between extent of lesion and amount of practice for the animals in this series is $p = 0.24 \pm 0.15$. Corrected for cases with motor disturbance, there remains no significant difference in learning ability between animals with slight and animals with extensive brain injuries.

In a more recent study (1926) I reported experiments on the influence of lesions within the area striata upon the animal's ability to form a simple visual habit. Forty-eight animals were trained in brightness discrimination after cerebral lesions in the occipital region ranging from 3.5 to 43.9 per cent of the total area of the neopallium. The operated animals required 94 per cent as much practice as normal animals trained under similar conditions. In relation to its probable error this difference is not significant. The correlation between extent of lesion and amount of practice required for learning in this series was $p = 0.11 \pm 0.14$. These figures justified the conclusion that the capacity to learn the habit of brightness discrimination is unaffected by any injury to the occipital half of the cerebrum, even including the entire area striata of both hemispheres.

Further data on these two problems indicated that when normal animals which had learned the habits were subjected to cerebral lesion in restricted areas, the habits were lost (Hunter, 1926; Lashley, 1927), in which case they could be reacquired by an amount of practice not exceeding the range for normal animals.

In contrast to this, loss of the maze habit following cerebral lesions proved to be attended by great difficulty in relearning, sometimes by total inability to reacquire the habit. This opened a new method of attack upon the problem of deterioration after brain injury and called for a more extensive investigation of the whole question.

PROBLEMS AND SPECIAL METHODS

In planning the experiments the following questions seemed most pressing:

1. Are there situations for the rat in which a deterioration of learning ability after brain injury can be demonstrated, as well as those, like the double-platform box, in which no defect appears? If so, what determines the involvement or non-involvement of the capacity to acquire each particular activity? To test this, it was desirable to sample as many different activities as possible; and in preliminary experiments the multiple choice method of Yerkes (1916), the perseverance reaction of Hamilton (1916), the alternation problem of Carr (1917), a variety of latch boxes, pattern vision, and several tests of direct adaptation to changes in the maze were tried out, in addition to the problems finally selected.

2. Is the deterioration following cerebral lesion temporary or permanent? To test this it was necessary, when reduced learning ability had been demonstrated for one type of problem, to train upon another similar problem at a later date, allowing at least a sufficient interval for complete recovery from any shock or diaschisis effect.

3. What is the influence of the locus of injury upon the capacity to learn different types of problems? This necessitates testing the effects of lesions in all possible parts of the cortex upon the learning of a variety of problems.

4. What is the effect of the magnitude of the lesion upon various types of learning? This requires lesions of different magnitude in each of the areas studied.

5. What is the relation between the sensory components of the problem, the locus of injury, and the degree of deterioration? To test this it was desirable to present problems offering different and controllable sensory cues.

6. What is the relation between the complexity of the habit and the degree of retardation after brain injury? To test this it was desirable to include several problems having the same sensorimotor basis and differing in the number of identical components included in each. Mazes most nearly meet this requirement but present the difficulty that one must either vary the pattern considerably, and so introduce other factors than the re-

duplication of parts, or risk obscuring results by permitting a large amount of transfer from one to another.

7. Is the capacity to remember affected in the same way as the capacity to learn? This calls for retention tests for the different types of situations studied.

8. When deterioration exists, is it due to sensory defect, to reduced motor control, to lowered efficiency of the mechanism of fixation, to a general functioning at a lower level of complexity, or what not? These questions demand a variety of tests and controls beyond immediate experimental possibility. They determined the inclusion of two problems, reversal of Maze I and the incline box, as tests of plasticity and of kinaesthesis.

It was desirable to observe the behavior of the same animals in a variety of situations, since only so could the effects of the same lesions in different situations be tested. This limited the number of problems which could be used to the capacity of the most retarded cases and made it necessary to discard the major-ity of the problem situations which were included in the prelim-inary tests. Most of these either required too great time for learning or failed to provide a clear-cut objective criterion of learning.

Ten problems were finally selected for study. To test the in-fluence of complexity of problem on degree of deterioration three mazes were used; and for the permanence of defect, a fourth. For diversity of sensory components the brightness habit and the incline box were included. Retention tests for two mazes and the brightness habit, and a test for the ease of substituting one habit for another, completed the series. A detailed description of the problems follows.

1. *Maze III.*—This is a maze with eight culs-de-sac requir-ing alternate right and left turns in the true path (Fig. 2). It is arranged for automatic recording of errors. The animals were given 5 trials per day until 10 consecutive errorless trials were obtained. Time consumed and errors per trial were recorded. In case learning was much retarded, training was discontinued after 150 trials, which is more than seven times the average re-quirement of normal animals, and almost twice the upper range of normal cases.
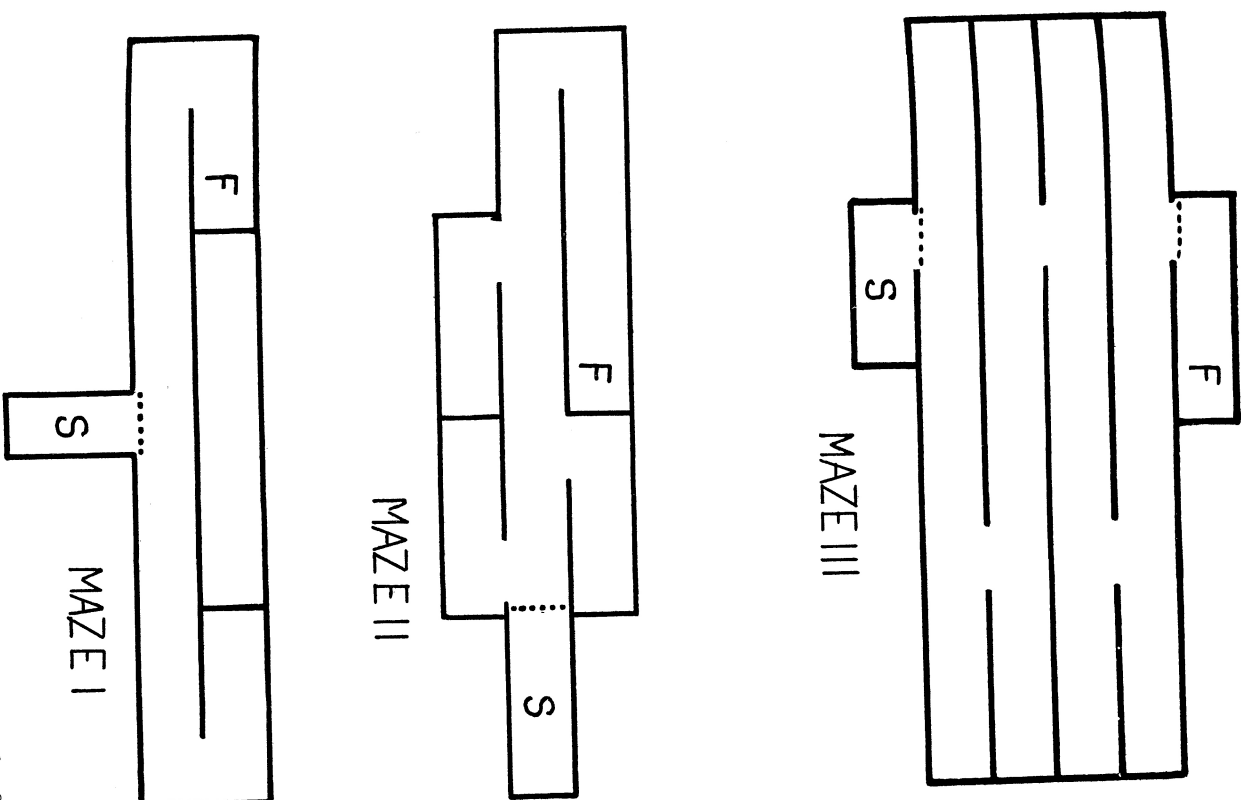
FIG. 2.—Ground plans of the inclosed mazes used in the present study. S, starting compartments; F, food compartments. The broken lines represent trap-doors which prevent return to the starting-box. Scale, 1 inch equals 1 foot.

2. *Maze II.*—This is a relatively simple maze having a straight path, with three culs-de-sac and the food compartment opening at the sides (Fig. 2). Training was continued at 5 trials per day until 10 consecutive errorless trials were obtained, or until 100 trials had been given. The latter is six times the average requirement for normal animals and three times the upper range of normal cases.

3. *Maze I.*—This is a simple **T** maze with one cul-de-sac to the right and food to the left (Fig. 2). With it, training was continued at 5 trials per day until 10 consecutive errorless trials were obtained, or until 60 trials had been given. The latter is four times the average requirement of normal animals and twice the upper limit of the range.

4. *Brightness discrimination.*—Animals were trained in a standard Yerkes box (Fig. 3) to choose the illuminated and avoid the darkened compartment. Training was continued at 10 trials per day until 30 consecutive errorless trials were obtained. No animal failed to reach this requirement.

5. *Retention of Maze III.*—Forty days after the completion of training on Maze III the animals were returned to it for tests of retention. These were given as were the original training tests and were continued to 10 consecutive errorless trials, or until 35 trials had been given. This is eighteen times the average requirement for relearning by normal animals and seven times the upper limit of their range.

6. *Retention of Maze I.*—On completion of retention tests for Maze III, a similar series was given for Maze I, with 5 trials per day to 10 consecutive errorless trials, or until 35 trials had been given. The latter is seven times the average requirements of normal animals and three times the upper limit of the normal range.

7. *Reversal of Maze I.*—After completion of the retention tests for Maze I the food was transferred to the cul-de-sac on the right and the animals trained to turn to the right and avoid the former correct path. Training was continued at 5 trials per day to 10 consecutive errorless trials, or until 50 trials had been given. The latter is four times the average requirement of nor-

mal animals and nearly three times the upper limit of their range.

8. *Retention of brightness discrimination.*—Retraining tests were given in the discrimination box until 30 consecutive errorless trials were obtained.
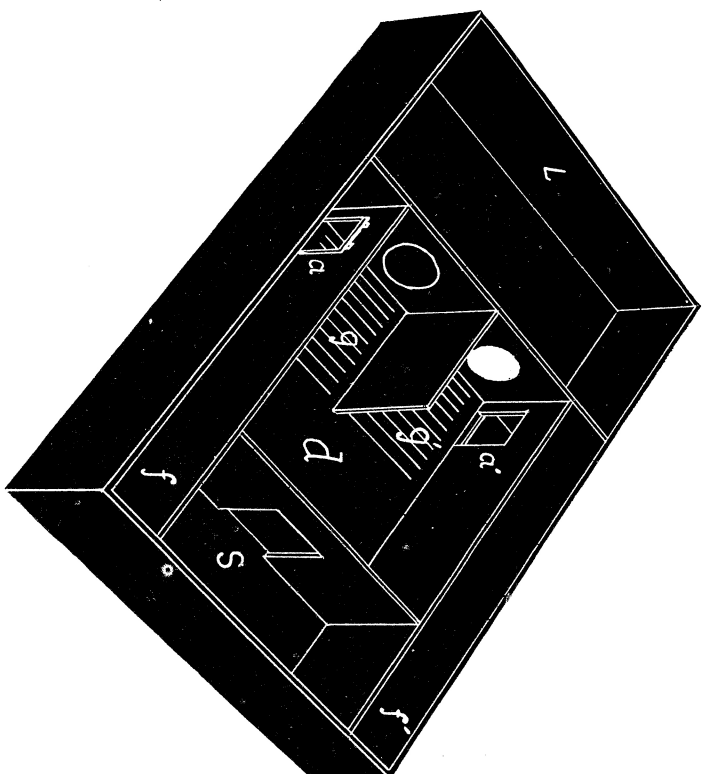
Fig. 3.—Box used for training in brightness discrimination. The animal is started at S and passes to d, where a choice of an illuminated and dark alley is offered. These lead across electric grills (g, g') through trapdoors of light celluloid (a, a') to the food compartments (f, f'). In training, the door on the dark side is locked and the grill charged. The illumination is shifted irregularly from side to side by a movable screen in the light-box (L). In use the entire box is covered except for an observation hood above d.

9. *Maze IV.*—This maze has the general plan of Maze III, reversed (Fig. 4), but requires the animal to run along the edges of vertically placed boards, $\frac{3}{16}$ inch in width, after the method devised by Miles (1927). Animals were given 5 trials per day to 10 consecutive errorless trials, or until 60 trials had been given.

en. The latter is nine times the average requirement of normal animals and three times the upper limit of their range.

10. *Incline box.*—As a test of the possible loss of somesthetic sensitivity some of the more deteriorated of the operated cases were trained in a problem box which required discrimination of the direction of slope of an inclined surface. The problem box is of essentially the same form as Maze I, arranged so that it
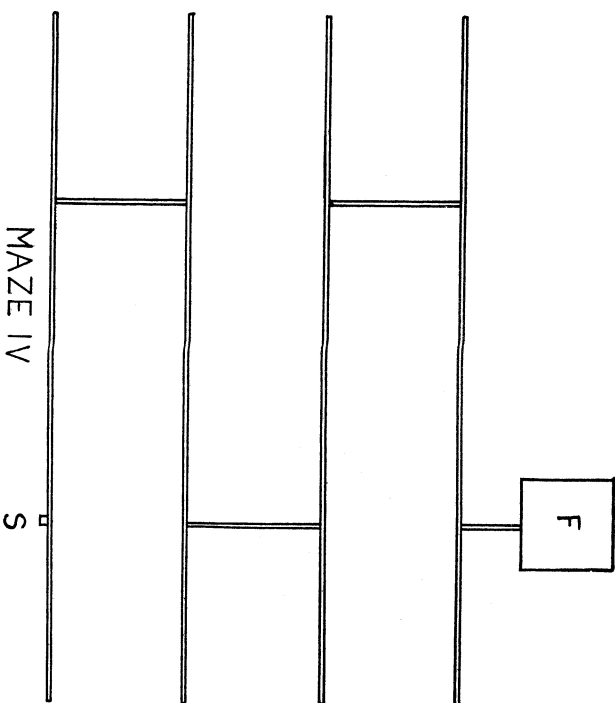
MAZE IV

F

S

FIG. 4.—Ground plan of open maze. This was constructed of $\frac{3}{16}$-inch boards set on edge and supported 2 feet above the floor. S, starting-point, F, feeding-platform.

may be tilted laterally at an angle of 12½° with either end elevated above the other. The box is inclosed, light-tight, and the alleys wired with punishment grills and with signal contacts which record the animal's position. The animals were trained to turn up the incline on leaving the starting-compartment. Ten trials per day were given until 30 consecutive errorless trials were obtained.

The animals were trained successively in these problems in the order in which they are listed above. In the majority of cases

training in each problem was begun immediately upon the completion of the tests with the preceding problem, but with some of the cases having more extensive lesions, which lose weight under the conditions of training, it was necessary to introduce a rest period of a week or more between problems.

Hunger was used as the incentive in all the mazes; a combination of hunger and electric shocks in the discrimination habits.

Fifty animals were subjected to cerebral lesion and started on the series of problems at an interval of from 10 to 30 days after operation, depending upon the rate of recovery from operation. Thirteen were discarded because of illness in the early stages of training or because of evidence of infection of the brain tissue at necropsy. Others died during the course of the experiment so that only 21 completed the series of problems. In addition 22 normal animals were started in the series of problems under similar training conditions. Six of these died during an epidemic of dysentery before completion of the series.

When symptoms of illness developed in any animal, training was discontinued immediately, and his record for the problem last completed was discarded, as a control of the effect of earlier undetected illness. Thus in Table I the animals recorded as dead after learning Maze III had completed Maze II, and so on.

The complete records for the operated animals are given in Table I and diagrams of the lesions in Plates I–IV, Figs. 1–37. In this series are included six animals which had been trained in brightness discrimination before operation and which therefore lack data on this problem. There is no indication of any influence of their previous training upon their records in this experiment. The records of the normal controls are given in Table II. Upon the data included in these two tables the following analyses are based.

DETERIORATION OF OPERATED ANIMALS SHOWN BY
MASSED RECORDS

We shall first consider the average effects of cerebral lesions, disregarding locus and magnitude; then examine more closely

TABLE I

Individual Records of Learning or Retention in 10 Problems, Made by Animals after Cerebral Lesions. The Percentage of the Total Neopallium Destroyed Is Given at the Left. Diagrams Illustrating the Lesions Are Given under Corresponding Numbers in Plates I–IV. Total Time Spent in Practice, Total Errors during Training, and Total Trials Preceding the 10 Consecutive Errorless Trials (30 in Discrimination Experiments) Are Given for Each Animal

No.	Percentage of Destruction	Maze III Time (in Seconds)	Maze III Errors	Maze III Trials	Maze II Time (in Seconds)	Maze II Errors	Maze II Trials	Maze I Time (in Seconds)	Maze I Errors	Maze I Trials
1	1.5	111	5	3	20	2	3	74	9	28
2	4.6	2,388	51	17	185	13	22	107	8	22
3	6.0	8,842	126	47	340	24	19	0	0	0
4	7.3	5,007	92	36	214	24	16	135	12	29
5	7.9	2,131	112	62	134	10	10	79	5	16
6	8.0	901	82	61	47	7	11	33	6	9
7	8.4	2,357	43	31	45	4	4	23	1	1
8	9.1	4,039	65	28	678	39	19	125	12	27
9	11.2	4,321	165	51	390	28	26	94	7	13
10	16.1	3,304	397	120	170	18	15	75	18	18
11	16.4	1,972	338	77	236	33	50	36	4	5
12	18.1	2,520	163	77	822	81	23	0	0	0
13	22.6	5,108	332	54	410	54	33	108	27	36
14	22.8	2,457	534	150 (23)*	157	34	42	67	20	1
15	23.0	4,235	183	59	78	7	12	292	38	39
16	23.9	13,567	621	86	506	51	100	471	61	60
17	24.8	3,799	388	90	286	39	34	83	11	12
18	24.9	1,232	206	59	281	20	22	136	17	17
19	25.3	1,254	147	37	345	41	60	52	7	16
20	26.9	11,931	752	150 (57)	1,280	273	100	756	91	60
21	27.6	3,130	309	100	133	15	14	203	33	60
22	27.9	5,207	444	150 (2)	253	30	18	0	0	0
23	29.5	6,117	331	62	Died					
24	30.6	3,314	501	150 (0)	451	94	68	856	45	60
25	32.0	3,128	193	60	392	31	43	277	30	51
26	34.8	3,767	645	150 (0)	292	67	56	23	6	3
27	39.8	12,909	617	73	291	59	86	172	52	60
28	41.5	7,785	546	64	122	26	11	0	0	0
29	44.8	14,121	809	106	541	90	91	156	23	22
30	44.9	4,048	386	150 (0)	212	17	12	132	26	32
31	53.3	4,622	682	150 (0)	Died					
32	54.9	9,561	761	111	1,129					
33	57.6	8,284	593	135	423	64	82	11	1	1
34	65.3	17,142	2,287	150 (0)	1,955	66	51	115	23	28
35	66.4	5,885	1,048	150 (0)	3,186	470	60	1,000	18	13
36	69.5	15,479	1,423	150 (0)	Died					
37	81.2	18,224	1,330	150 (0)	667	75	40	22	2	4

* Figures in parentheses are errorless trials.

TABLE I—Continued

No.	Percentage of Destruction	Visual Discrimination Errors	Visual Discrimination Trials	Maze III Retention Time (in Seconds)	Maze III Retention Errors	Maze III Retention Trials	Maze I Retention Time (in Seconds)	Maze I Retention Errors	Maze I Retention Trials
1	1.5	21	60	4	2	1	65	7	15
2	4.6	39	90	300	10	1	5	1	3
3	6.0	18	70	Died					
4	7.3	40	140	674	61	6	80	8	16
5	7.9	Died							
6	8.0	46	130	135	9	18	0	0	0
7	8.4	30	80	1,347	38	10	15	1	1
8	9.1	Died							
9	11.2	43	120	131	3	5	124	7	14
10	16.1	33	160	30	5	3	89	6	8
11	16.4	22	100	4,018	433	35	14	2	4
12	18.1	10	30	289	40	26	163	2	2
13	22.6			431	51	35	153	33	35
14	22.8	38	100	334	20	35	0	0	0
15	23.0			303	39	35	42	5	11
16	23.9	24	80	5,810	580	35	194	35	35
17	24.8			402	48	35	256	44	34
18	24.9	97	200	75	9	6	7	1	2
19	25.3	48	170	1,423	152	35	128	24	31
20	26.9			306	41	35	F*	F	F
21	27.6			512	57	35	117	23	35
22	27.9						0	0	0
23	29.5	19	80	1,067	127	35	246	50	35
24	30.6			101	7	9	79	5	9
25	32.0	11	70	991	102	35	167	21	23
26	34.8			751	112	35	21	1	1
27	39.8	43	180	3,799	190	10	51	3	4
28	41.5	23	50	795	253	35	47	6	6
29	44.8	68	180	466	93	35	0	0	0
30	44.9	45	140	Died					
31	53.3			Died					
32	54.9	57	100	Died					
33	57.6	34	180	427	63	35	92	19	33
34	65.3	64	120	Died					
35	66.4	108	230	927	270	35	0	0	0
36	69.5	Died							
37	81.2	Died							

* "F" indicates cases which failed through inactivity

TABLE I—Continued

No.	Percentage of Destruction	Maze I Reversal Time (in Seconds)	Errors	Trials	Visual Discrimination Retention Errors	Trials	Maze IV Time (in Seconds)	Errors	Trials	Incline Box Errors	Trials
1	1.5	169	17	34	2	10	476	10	1	6	
2	4.6	52	5	6	0	0	4,868	26	14	6	20
3	6.0										
4	7.3	101	12	33	0	0	2,808	87	17		
5	7.9						3,113	17	7	14	40
6	8.0	65	15	29	3	10	1,290	27	4		
7	8.4	28	3	6	0	0					
8	9.1										
9	11.2	52	3	6	2	20	2,742	41	6		
10	16.1	351	29	37	9	50	10,792	255	9		
11	16.4	41	8	10	6	30	1,593	52	9		
12	18.1	289	24	38	2	10	5,865	339	60		
13	22.6	F*	F	F			4,666	481	60	17	40
14	22.8	264	50	50	0	0	2,494	93	32		
15	23.0	69	5	7			4,355	228	60	17	40
16	23.9	F	F	F	1	10	7,703	776	60	18	50
17	24.8	269	24	18			F	F	F		
18	24.9	102	7	18			1,858	89	16	9	20
19	25.3	53	10	16	2	20	2,370	52	22		
20	26.9	F	F		2	10	16,396	235	60	12	20
21	27.6	F	F	F			11,079	290	60	16	50
22	27.9	229	23	40			2,842	98	32		
23	29.5	F	F	F	0		3,116	106	60		
24	30.6	F	F	F			1,803	273	60	17	60
25	32.0	72	5	6	0						
26	34.8	175	22	26	1	10	6,985	321	60		
27	39.8	116	18	20	0	10	1,947	104	38		
28	41.5	120	20	38	6	30	8,024	412	60		
29	44.8	112	15	17	0	10	4,170	276	60		
30	44.9	266	42	50	1	0					
31	44.9										
32	53.3										
33	54.9	164	18	32	5	40	F	F	F		
34	57.6										
35	65.3	285	51	50	15	60	9,072	391	60	25	70
36	66.4										
37	69.5										

* "F" indicates cases which failed through inactivity.

TABLE II

Individual Records of Normal Animals Employed as Controls in the 10 Problems Used To Test Efficiency in Learning and Retention after Cerebral Lesions. Total Time in Seconds, Total Errors during Training, and Total Trials Preceding the 10 Consecutive Trials without Error Are Given

No.	Maze III Time	Errors	Trials	Maze II Time	Errors	Trials	Maze I Time	Errors	Trials
38	520	54	24	46	10	8	49	9	12
39	566	28	3	61	4	13	72	8	19
40	601	38	16	310	17	16	63	6	11
41	538	34	11	65	9	10	16	3	2
42	458	43	14	144	18	34	31	5	9
43	570	40	16	80	13	13	39	8	16
44	568	23	7	91	11	13	52	9	18
45	646	43	21	87	8	11	12	1	1
46	1,168	29	17	131	14	14	41	4	6
47	748	29	22	146	23	30	88	9	22
48	3,451	65	21	157	14	15	86	5	21
49	1,142	44	20	129	17	8	169	12	35
50	584	51	17	130	22	25	89	3	7
51	537	35	20	164	20	23	82	12	37
52	3,682	116	16	104	11	22	32	4	12
53	452	49	19	196	29	13	48	3	22
54	566	43	20	132	19	8	98	15	13
55	501	30	24	171	33	22	155	15	36
56	1,691	71	22	Died					
57	1,469	31	28	Died					
58	1,468	45	27	Died					
59	2,007	101	36	Died					

TABLE II—Continued

No.	Visual Discrimination Errors	Trials	Maze III Retention Time	Errors	Trials	Maze I Retention Time	Errors	Trials	Maze I Reversal Time	Errors	Trials
38	90	29	207	18	2	15	2	10	48	6	18
39	70	29	13	1	1	0	0	0	52	5	16
40	140	51	25	2	1	0	0	0	27	3	6
41	70	20	128	10	3	41	64	8	65	3	1
42	120	44	59	5	3	64	3	4	124	4	3
43	220	56	121	17	2	0	0	0	20	4	2
44	130	38	281	18	4	8	1	1	42	4	16
45	290	127	12	1	1	8	2	3	29	4	8
46	210	83	29	2	1	17	1	3	40	3	11
47	140	45	32	4	2	8	1	3	56	6	19
48	Died										
49	Died		41	0	0	9	2		48	5	16
50	Died										
51	90	31	56	4	5	11	2	6	76	6	12
52	90	40	58	4	1	23	3	13	89	8	16
53	Died										
54	220	64	18	1	1	23	3	12	42	5	11
55	30	16	250	16	4	41	3	8	116	8	29

TABLE II—*Continued*

No.	Brightness-Discrimination Retention		Maze IV			Incline Box	
	Errors	Trials	Time	Errors	Trials	Errors	Trials
38	0	0	1,566	25	7	....	....
39	20	5	678	26	9	....	....
40	20	3	964	6	2	....	....
41	0	0	1,088	23	15	....	....
42	0	0	2,181	56	7	....	....
43	20	2	1,449	9	2	....	....
44	0	0	1,592	45	8	....	....
45	40	7	1,860	33	1	....	....
46	20	4	1,591	30	21	....	....
47	10	1	1,856	31	3	....	....
48	....	....	....	....	....	....	....
49	30	4	281	8	3	7	30
50	20	0	2,270	49	7	5	20
51	0	3	1,097	23	4	4	20
52	....	....	....	....	....	....	....
53	0	0	610	8	2	7	20
54	10	1	599	26	6	5	20
55	....	....	....	....	....	....	....

the relative influence of these variables in determining the results. The average extent of injury in the operated cases was 31.1 per cent of the total surface area of the cortex, with a range from 1.5 to 81.2 per cent and a distribution covering every part of the cortex. Figure 5 shows the combined extent of the lesions.

The average scores, total time, total errors, and total trials have been computed for each problem for all normal and for all operated animals. In computing the constants, cases which failed through inactivity (marked "F" in Table I) have been omitted. These scores with their probable errors are summarized in Table III. In this table, under the heading "Difference" the absolute difference between the groups in time, errors, and trials is included. For convenience in comparison, the average percentage of the normal score represented by the records of the operated animals has been computed for each problem. This was determined by expressing each score (time, trials, errors) of the operated group as a percentage of the corresponding score of normals, then computing the average of these percentages for each problem. These average differences are shown graphically in Figure 6

INCLOSED MAZES

Turning first to a comparison of the data for the three inclosed mazes, we find that, in initial learning, the operated animals are significantly inferior to the normal controls. For the most complicated maze (III) the operated animals required six and one-half times as much practice as normals, and not all upon which this average is based completed the problem. For the simple mazes the differences are less striking, but even for the simplest maze the operated required more than twice as much practice as the normals. T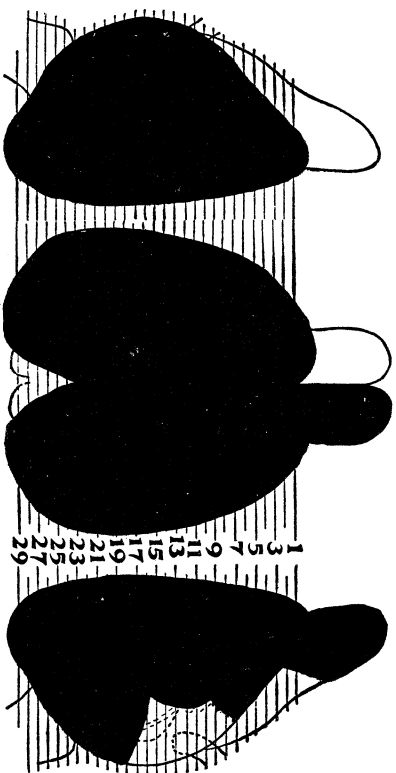he differences are statistically significant, being on the average eleven times their probable errors for Mazes III and II and almost five times the probable error for Maze I. From this there can be no question that the cerebral lesions were attended by an increase in the amount of practice necessary to attain the required facility in running the maze.

For the breaking-up and reversal of the original habit of Maze I the ratio of practice for operated and normal animals is about the same as that for initial learning of the same maze (2.8:1) and statistically somewhat more reliable. Inspection of the individual records for this maze shows a rather peculiar condition. Some of the animals with extensive lesions learned it without a single error, thus excelling any normal animal. Of

Fig. 5.—Combined extent of the lesions in animals trained after operation. In one or another, every part of the neopallium was destroyed.

TABLE III

COMPARISON OF THE AVERAGE RECORDS OF NORMAL ANIMALS AND OF ANIMALS WITH CEREBRAL LESIONS IN 10 PROBLEMS. THE AVERAGES ARE BASED UPON ALL ANIMALS IN EACH GROUP WHICH REACHED THE CRITERION OF LEARNING OR COMPLETED THE ARBITRARY NUMBER OF TRIALS AT WHICH TRAINING WAS DISCONTINUED. UNDER "DIFFERENCE" THE ABSOLUTE DIFFERENCE BETWEEN THE GROUPS IS GIVEN, AND UNDER "PERCENTAGE" THE AVERAGE OF TIME, ERRORS, AND TRIALS OF THE OPERATED GROUP IS EXPRESSED AS PERCENTAGE OF THE CORRESPONDING AVERAGE OF NORMAL ANIMALS

PROBLEM	NORMAL			OPERATED			DIFFERENCE			AVERAGE DIFFERENCE AS PERCENTAGE OF NORMAL RECORD
	Time (in Seconds)	Errors	Trials	(Time (in Seconds)	Errors	Trials	Time (in Seconds)	Errors	Trials	
Maze III.........	1,087± 78	47±2	19± 1	5,680±460	460±42	91±5	4,593±466	413±42	72± 5	655
Maze II..........	135± 10	16±1	16± 1	541± 29	78± 4	42±4	406± 30	62± 4	26± 4	377
Maze I...........	64± 7	7±1	17± 2	183± 13	22± 3	24±3	119± 15	15± 3	7± 4	245
Visual discrimination............	....	41±6	135±12	....	41± 3	119±7	....	0± 7	16±14	94
Maze III relearning	86± 9	7±1	2± 0.2	1,001± 51	91± 6	21±2	915± 51	84± 6	19± 2	1,165
Maze I relearning..	18± 2	2±0.3	5± 1	79± 12	11± 2	14±3	61± 12	9± 2	9± 3	478
Maze I reversal....	58± 3	5±0.2	12± 1	150± 21	19± 2	26±2	92± 21	14± 2	14± 2	287
Visual discrimination relearning...	....	2±0.5	13± 2	....	3± 0.5	15±2	....	1±0.7	2± 3	127
Maze IV..........	1,365±115	26±3	7± 1	5,697±610	207± 25	39±4	4,332±620	181±26	32± 4	599
Incline box.......	....	6±0.2	22± 1	....	14± 2	40±3	....	8± 2	18± 3	217

these, the ones which survived for the tests of reversal of the habit, and others also which made perfect scores in retention tests for Maze I, had unusual difficulty in breaking up the habit of turning left and acquiring that of turning to the right in this maze. Taking the group as a whole, we find a slight negative correlation between the amount of practice required for learning Maze I and for reversal of the habit. This, in conjunction with observations of the behavior of the animals during training, suggests that some of them came to the problem with a definite set for turning in one or the other direction, perhaps transferred from the more complex mazes, and that this was largely influ-
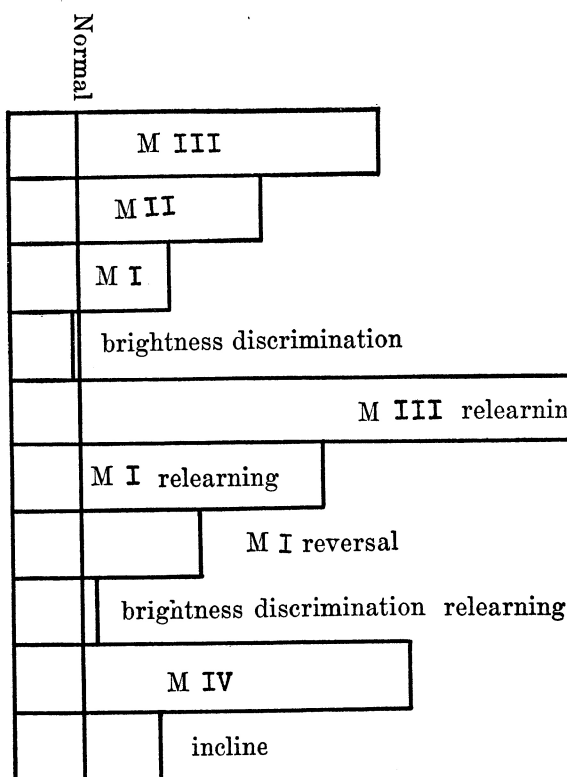

FIG. 6.—Comparisons of the averages of normal and operated animals in the 10 problems in which they were tested. The average of operated animals is shown as percentage of the normal average, indicated by the continuous line marked "normal."

ential in determining the success with Maze I. The variability of the results seems largely due to such transfer, but it is doubtful whether this has significantly altered the difference between normal and operated animals. The preferences for the right or left should have averaged out between the initial training and reversal of the habit, and we find the operated equally inferior to the normals in both.

The slight negative correlation between learning and reversal of this maze, appearing among the operated animals and not among the normal controls, suggests that the operated animals may have a somewhat greater tendency toward preservation than have the normals. The magnitude of the negative correlation and the number of cases are both too small to establish this conclusion.

The relearning tests after 40 days show even greater differences between the normal and operated cases than do the records of initial training. Relatively few of the cases with more severe lesions relearned Maze III in 35 trials, which is almost twice the average for *initial* learning of normals; and the average practice spent in retraining tests was more than eleven times the corresponding average for normals. The differences are on the average fourteen times their probable errors. For relearning of Maze I the difference is less pronounced but nearly twice as great as that which appeared in initial training.

There is clear evidence that the operated animals were inferior to the normal controls in all tests with the inclosed mazes. Since they were trained successfully on the different mazes, elements of transfer and interference almost certainly entered into the results. There is at present no way of judging the relative influence of these factors on the scores of normal and of operated animals, but certainly there is no reason to believe that differences with respect to transfer between normal and operated animals are to any great extent responsible for the absolute differences in their records on any single maze.

The open maze (IV) presents an objective complexity identical with that of Maze III. It was, however, learned by both

normal and operated animals in less than half the practice required for the inclosed maze, as judged by trials or errors, although the time consumed was about the same for both mazes. This more rapid learning may have been due either to the stronger incentive provided by the narrow and somewhat unsteady support or to the addition of a visual factor which rapidly gives general orientation.

In this maze the inferiority of the operated animals is about the same as for the similar inclosed maze (5.99:1), and the differences are on the average seven times their probable errors.

In some ways the most surprising outcome of the experiments is the marked difference in the effects of cerebral injuries upon the learning of the mazes and of brightness discrimination. Some retardation appears in the experiments with all the mazes, yet some animals which failed to learn Maze III in eight times the practice required by normals were superior to the normals in the formation of the habit of brightness discrimination. This result is consistent with my earlier finding (1927) that complete destruction of the posterior third of the cerebrum, including the entire visual cortex, effected no retardation in the formation of the habit of brightness discrimination. As a further check upon it the following experiment was carried out.

Thirteen animals which had been used to test the influence of lesions upon the previously formed maze habit (see the experiments on localization of the maze habit reported in a later section) and which had made very poor records in relearning the maze were subsequently given initial training in the habit of brightness discrimination. Their records for maze relearning and for the visual habit are compared in Table IV. For relearning the maze they required five times as many trials as are required for initial learning by normal animals, thus giving evidence of a serious retardation. One of them failed to learn the visual habit through inactivity. The average of the others is slightly better than that of normals trained under similar conditions. The brain lesions, which are shown in Plates V–IX under numbers corresponding to the numbers of the animals in the

table, produced no effect upon the ability to form the visual habit, although they had abolished the maze habit and produced a severe reduction in the capacity to relearn it.

An understanding of the difference between the results with the mazes and the visual habit will require the weighing of a number of considerations. Inequalities in incentives, in the complexity of the habits, in the sensory mechanisms involved, or in

TABLE IV

COMPARISON OF POSTOPERATIVE RETENTION TESTS FOR THE MAZE IN SOME ANIMALS SHOWING DEFINITE RETARDATION AFTER OPERATION WITH THE RECORDS OF THE SAME ANIMALS MADE SUBSEQUENTLY IN LEARNING THE HABIT OF BRIGHTNESS DISCRIMINATION

No.	Postoperative Retention Tests (Maze)			Visual Discrimination, Initial Learning	
	Time (in Seconds)	Errors	Trials	Trials	Errors
1	83	1,839	306	107	60	21
2	86	1,004	226	45	40	7
3	88	3,182	341	114	40	14
4	91	3,288	574	106	120	56
5	95	5,607	900	131	130	38
6	105	3,222	602	150	50	18
7	106	6,247	387	55	180	36
8	110	2,230	127	48	*	*
9	111	1,282	166	44	240	102
10	113	2,364	333	115	90	33
11	117	11,111	1,689	150	140	66
12	118	5,917	1,122	150	70	21
13	119	1,659	212	50	130	46
Average		3,765.5	537.3	95.0	107.5	38.2
Average of normal animals					135	41

* Failed through inactivity.

the character of the motor adjustments required may have been responsible for the differences. Only the first of these can be evaluated before the presentation of other evidence. In the visual habit, both hunger and punishment for errors were used to establish the habit; in the mazes, hunger alone. This suggests that the operated animals may either be lacking in appetite or be hyperalgesic. Their general behavior bears out neither sup-

position. They are in general more eager for food and more greedy in eating than the controls, whereas their responses to punishment are less pronounced and often suggest a considerable degree of analgesia. More convincing evidence against the importance of punishment in this connection is given by the results of earlier studies with the double-platform box. In this no punishment was used, yet the problem was learned equally readily by normal animals and by those with as much as 50 per cent of the cortex destroyed. This throws us back upon some other explanation of the difference between the results with the mazes and brightness discrimination. We must postpone further discussion of this question until data upon the relation of retardation of learning to sensory factors and to the complexity of the problem have been presented.

Not enough cases were trained on the incline to make the results of much value. The habit is formed very quickly both by normal and by operated animals, and it is doubtful whether the difference is significant. I have not used this problem long enough to acquire a dependable technique and so am not inclined to give it weight. However, there is no indication of a retardation comparable to that in Mazes III and IV; and since this habit depends upon kinaesthesis to an even greater extent than the mazes, the results may serve as contributory evidence upon the sensory factors in the maze.

CONCLUSIONS

This comparison of the massed records of normal and operated animals brings out two facts clearly. (1) The operated animals are significantly inferior to normals trained under similar conditions in the learning and retention of a variety of mazes. (2) The inferiority is not uniform but is statistically reliable for all the mazes. In contrast to this, there is no evidence of any inferiority in the formation or retention of the habit of brightness discrimination. In all cases where operated and normal animals have been compared in initial learning of this habit, the operated animals have been slightly superior to normal controls, although the differences in any one experiment have not been

statistically valid. The results justify the conclusion that cerebral lesions may produce a marked reduction in the ability to learn and to remember some problems and at the same time leave the capacity with respect to other problems entirely unaffected.

PERMANENCE OF THE DETERIORATION

The records of the first four problems show a progressive decrease in the inferiority of the operated animals until in the brightness habit they slightly excel the normals (Fig. 6). This looks like an improvement in learning ability with recovery from the effect of operation, but the fallacy of such an interpretation is shown by the records of the next problem, retention of Maze III. Here the operated animals consumed more than ten times the practice required by normals, and no animal which had failed to attain the criterion of learning in the initial training succeeded in learning in the retention tests, although these involved twice as many trials as are required for initial learning by normal animals. A similar inferiority appeared in the relearning and reversal of Maze I, although, as in initial learning of this maze, the difference was less pronounced than for Maze III. In the next problem, retention of the brightness habit, the inferiority practically disappeared. Finally, in learning Maze IV, the inferiority of the operated animals reappeared to almost as great an extent as in the first trials with Maze III immediately after operation.

The tests with Maze IV were begun at an average of 83 days after operation, with a range from 45 to 189 days. According to Donaldson's interpretation of the rate of development of the rat (Donaldson, 1924) this average corresponds to nearly 7 years and the maximum period to 15 years in the human span of life. Although we cannot use this comparison as a basis for any certain judgment of the stability of deterioration, it does give an indication of the duration of the unimproved condition in relation to the total span of life of the animal. There is no evidence for any improvement in learning ability during the time that the animals were kept under observation. On the contrary, the data show that the inferiority persisted during 3–6 months and was at

all times marked for some problems and not for others. This constitutes evidence that the deterioration of the operated cases is not due to temporary shock or to any diaschisis effect but is a residual condition, ascribable by Monakow's criteria (1914) directly to the absence of the tissue destroyed.

THE INFLUENCE OF THE LOCUS OF INJURY UPON RETARDATION IN LEARNING

The series of cases includes animals with lesions in various parts of the cerebrum. In view of the emphasis which has been
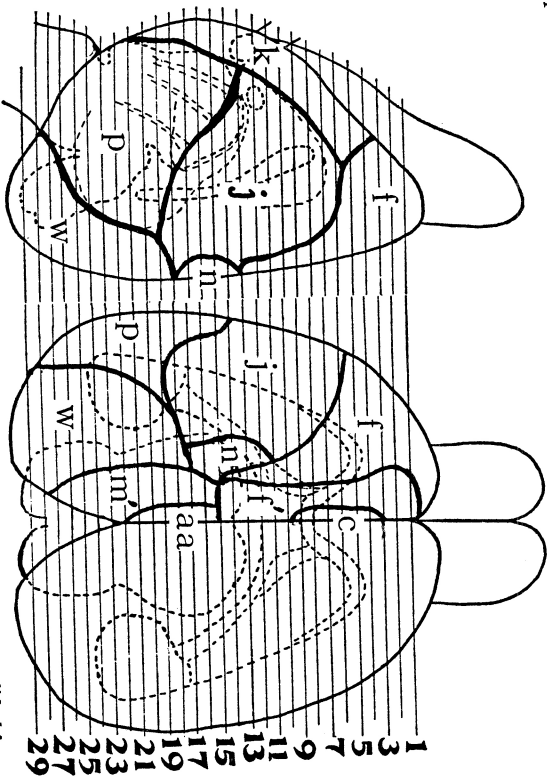

FIG. 7.—The chief cyto-architectural areas of the rat's cerebrum, modified from Fortuyn (1914) to the proportions of our diagrams. For significance of letters, see text.

placed upon association areas and upon image types in human learning, it seemed improbable that injuries in different areas should be equally effective in producing retardation of learning. We should expect either specific types of retardation associated with sensory defects or retardation following only the destruction of definite association areas. The rôle of sensory defects will be considered later. We must first consider the influence upon learning of lesions in the different cortical areas. Figure 7 shows the chief cortical regions distinguished by

Fortuyn (1914) on the basis of cell lamination. It has been necessary to modify the proportions of his diagram to fit the one used in these studies. Since the dorsal and lateral surfaces of the cortex offer no clear landmarks and Fortuyn does not show the relation of his fields to the underlying subcortical structures, the adaptation could be made only in terms of the relative proportions of our figures. This means some uncertainty as to the boundaries of the fields, but probably no more than would exist after the accurate mapping of any single brain, since the transition from field to field is, for the most part, gradual through a broad transitional zone and, if we may argue from the condition in man, there is considerable individual variation in the limits of the different fields.

Homologies with higher forms suggest that fields f, f', and n correspond to the motor or pyramidal region, and w and m' to the visual areas of higher animals (Herrick, 1926, pp. 159–65).

The percentage of the cortex, by our method of measurement, included in each of these functional groups of fields is the following:

f, f', c, and n (motor) 17.9
j (somesthetic) 27.6
p (auditory) 28.1
w, m', aa (visual) 19.2
k (olfactory)* 7.2

The cases of Table I have been divided according to the chief cyto-architectural areas involved. It is possible to distinguish, for statistical treatment, a frontal group in which the lesions extend more or less completely over areas f, f', and c and overlap j to only a very slight extent; a temporal group restricted chiefly to areas j, with some involvement of p but without overlapping f, f', or w; an occipital group covering areas w, m', and aa, invading p slightly but without involvement of j or f'; two cases with lesions restricted to p only. In addition there are cases with

* The chief olfactory cortex is the hippocampus, which was injured in a number of animals. I have not attempted to measure accurately the extent of injury to the hippocampal structures, but rough estimates of the extent of lesion indicate that this omission has not seriously influenced results.

smaller lesions restricted to f, j, or w which can be used to test the significance of the overlapping.

The constants derived from each of the foregoing regional groups are given in Table V for Maze III. The averages for time, errors, and trials are given separately and are also combined in

DATA FOR MAZE III

TABLE V

THE INFLUENCE OF REGIONAL DIFFERENCES IN THE POSITION OF CEREBRAL LESIONS UPON THE RATE OF LEARNING MAZE III. THE CASES ARE GROUPED ACCORDING TO THE PRINCIPAL ANATOMICAL AREAS INVOLVED. THESE ARE INDICATED BY LETTERS CORRESPONDING TO THE DESIGNATION OF THE AREAS IN FIGURE 7. THE LETTERS IN PARENTHESES INDICATE THE AREAS WITH WHICH THERE WAS SOME OVERLAPPING. THE GROUP MARKED "TRANSITIONAL" INCLUDES CASES WITH LESIONS CENTERING AROUND "w" AND INVADING PRACTICALLY ALL THE FIELDS

AREA	NO. OF CASES	PERCENTAGE OF DESTRUCTION	TIME (IN SECONDS)	ERRORS	TRIALS	AVERAGE PERCENTAGE NORMAL	CORRELATION Trials	CORRELATION Errors
f, f', c (j)	5	19.3	3,049	322	83	468	0.90	0.80
j (p)	4	24.7	3,559	265	67	414	0.80	0.80
w, m', aa (p)	7	21.9	7,062	371	96	649	0.73	0.88
w, m', aa, j	10	30.1	5,893	383	81	594	0.55	0.68
p	2	6.5	2,372	47	24	148	0.78	. . .
Transitional	7	24.8	5,554	354	58.1	521	. . .	. . .
Normal	16	0.0	1,087	47	19	100	. . .	. . .

a single expression as the average percentage of the corresponding records for normal animals. The number of cases in each of these groups is small, so that the averages are not very reliable. They serve, however, to indicate trends; and, in fact, the differences in most cases are of such magnitude as to be of unquestionable significance.

Auditory region.—The two cases (Fig. 8) with lesions restricted to area p (auditory) had only small injuries, amounting to not more than one-fourth of the entire area, and a rate of learning not significantly higher than that of normal animals. They are not adequate for a test of the function of area p, but do serve as a control for the two groups w (p) and j (p), both of

which overlap area p to an extent not greater than this. Retardation in these two groups could not have been due to the fact that both involve area p to a slight extent.
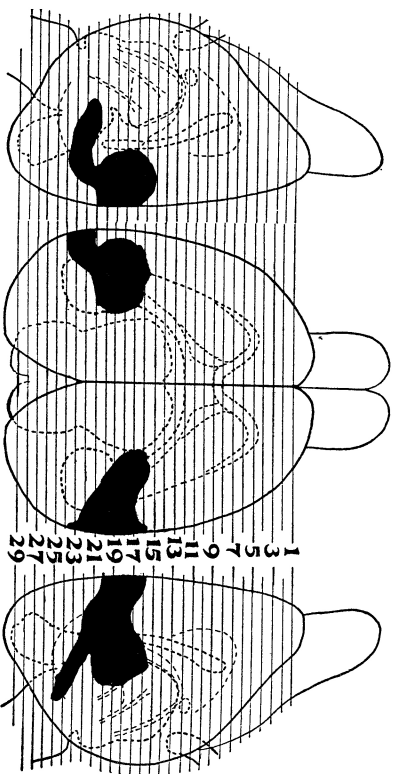

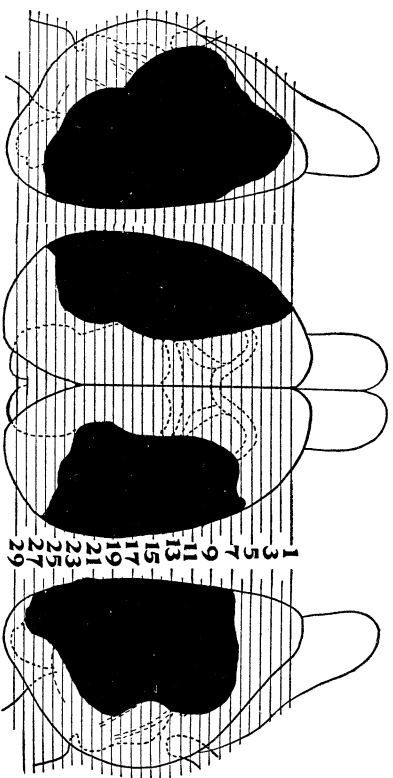Fig. 8.—Extent of lesions restricted chiefly to the auditory area (p)

Fig. 9.—Total extent of lesions involving chiefly the somesthetic area (j), with some overlapping of the auditory and visual areas.

Somesthetic region.—Cases with lesions restricted to j (somesthetic) and p (Fig. 9) required more than four times normal practice. The slight involvement of area p in these cases is probably not significant, and the data indicate that retardation may result from injury to j.

area p.

Visual area.—Cases with lesions in area w (visual) overlapping p slightly (Fig. 10) required six and a half times normal practice. The lesions did not greatly overlap fields f' or p. This retardation cannot be ascribed to the injury to area p.
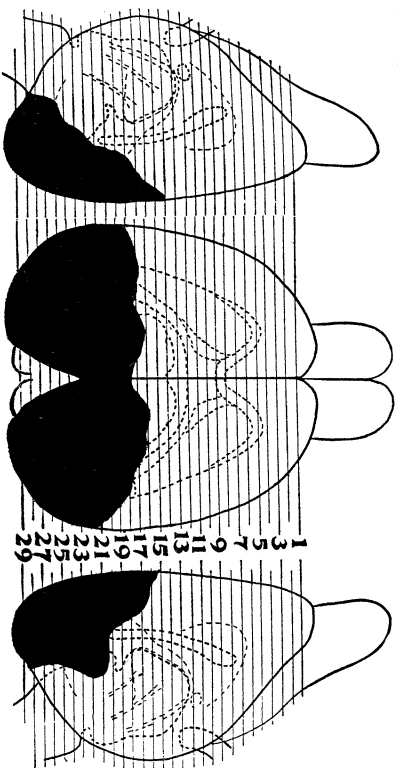
Fig. 10.—Total extent of lesions involving chiefly the visual areas (w, w')
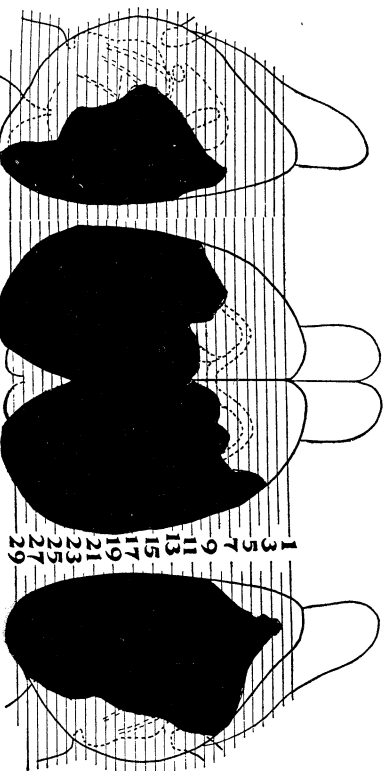
Fig. 11.—Total extent of lesions involving both visual and somesthetic areas (w and j).

Visual and somesthetic areas.—Cases with injuries involving both areas w and j (Fig. 11) required almost six times normal practice. The lesions did not greatly overlap fields f' or p.

Motor region.—Cases with lesions in the frontal area, f (i) (Fig. 12), required four and one-half times as much practice as

normals. The overlapping on area *j* was slight; and one case (No. 11), with 16 per cent destruction and no involvement of area *j*, required four and one-third times normal practice. We must conclude, then, that retardation is produced by lesions in the frontal (motor) field.

Transitional region.—It will be noted on Fortuyn's diagram that most of the cyto-architectural fields approach each other very closely in the median parietal region, so that a small lesion may invade the motor, somesthetic, auditory, and visual areas
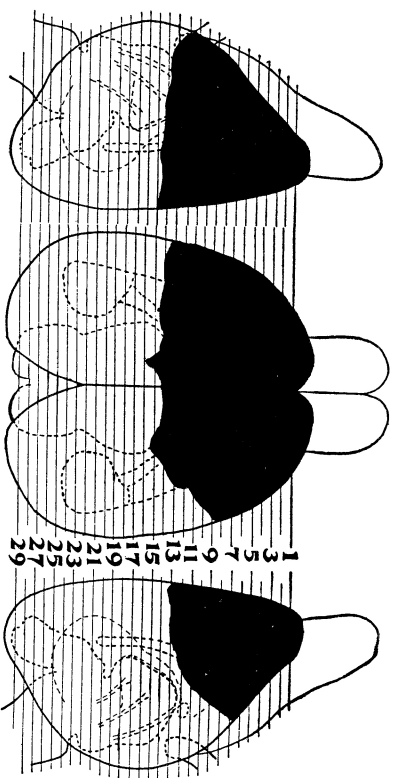
FIG. 12.—Total extent of lesions involving chiefly the motor region (*f*), with some overlapping of the somesthetic area (*j*).

A number of the cases have lesions centered in this region (Fig. 13); and since it might be interpreted as a primitive association area, these cases have been grouped separately, as "transitional." They required about five times as much practice as normals for learning.

Thus, injuries in any one of the four areas (motor, somesthetic, visual, transitional) for which adequate data are available produced a marked retardation. This ranges from 414 to 649 per cent of the amount of practice required by normal animals. These differences are great enough to be significant in spite of the small number of cases. They seem to prove that a lesion anywhere within these four areas may produce a marked retardation of learning for Maze III.

Relative effects of lesions to different areas.—The differences in effects of lesions within the three cortical areas are relatively very much smaller than their differences from the normal condition. The groups vary in the average extent of destruction, so that a direct comparison of the records for different areas is misleading. From the correlations presented in a later section we may compute the regression coefficients of time, errors, and trials on percentage destruction. These are for time, 139 seconds; for errors, 17.7; for trials, 1.9. That is, for each increment
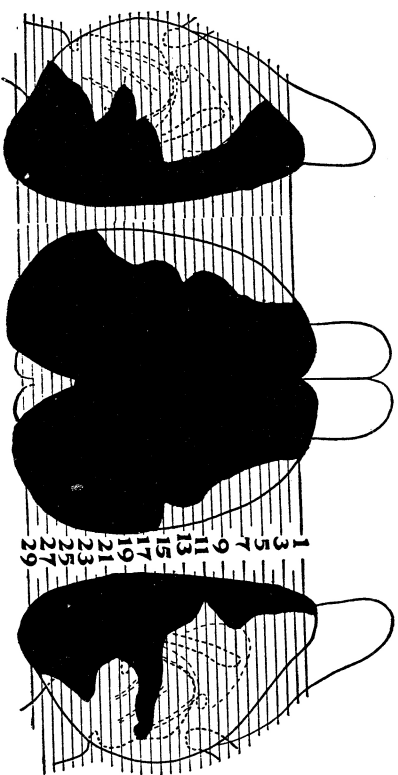

FIG. 13.—Total extent of lesions involving the transitional area.

of 1 per cent destruction we may expect an increase of 139 seconds, 17.7 errors, and 1.9 trials in the training record. Using these coefficients, we have computed from the records of normal animals the records to be expected from each amount of destruction. These have been expressed as average percentages of the averages for normals, with the following result:

Group	Motor	Somes-thetic	Visual	Visuo-somes-thetic	Auditory	Transi-tional
Experimental results..........	468	414	649	594	148	521
Computed from extent of lesion	484	597	570	705	145	598
Percentage of deviation from expectation................	−3	−31	+13	−15	+2	−14

This gives the actual deviation of the records of each group from the records to be expected if only the extent and not the

locus of injury is responsible for the retardation. For the motor, visual, visuosomesthetic, and auditory groups the differences are slight, amounting to not more than 15 per cent of the difference between the regional group and normal animals. Lesions within the somesthetic area apparently produced less effect than lesions within other areas. This may mean that the area is less important than the others for the formation of the maze habit, but I suspect that the result is due rather to an error in measurement of the lesions. As was pointed out in discussion of the reliability of the measurements, the region where there is the greatest chance for error is the dorsolateral zone covered by the diagrams of both lateral and dorsal aspects. Measurements are subject to error of perspective and to error in estimating the overlapping of the two diagrams. Lesions in area j mostly fall within this zone, and a constant error of 5 per cent in the measurement of lesions (sufficient to account for the deviation of this group from expectation) might easily have been introduced. We can only conclude that animals with lesions in the somesthetic field are distinctly inferior to normals, whereas their superiority over animals with lesions in other fields is doubtful.

The data include four cases with complete destruction of one hemisphere and partial destruction of the other. In two of these cases the intact cortex included only the right motor and somesthetic areas (Fig. 14); in the other two, the right visual and auditory (Fig. 15). The average records for each of these pairs were the following:

Region Preserved	Percentage of Destruction	Time (in Seconds)	Errors	Trials	Percentage of Normal Records	Computed Percentage
Right frontal........	67.9	10,682	1,285	150	1,500	1,135
Right occipital........	62.2	12,520	1,097	131	1,387	1,040

With very extensive but approximately equal amounts of destruction these two groups required almost exactly the same amount of practice for learning, in spite of the difference in the areas of the cortex which still remained intact.

We may approach the problem of regional differences in still another way. Only one of the 16 normal animals trained on

Maze III made more than 65 errors during training. We may therefore consider that 75 or more errors constitute some degree of retardation. There is no area common to the lesions of all
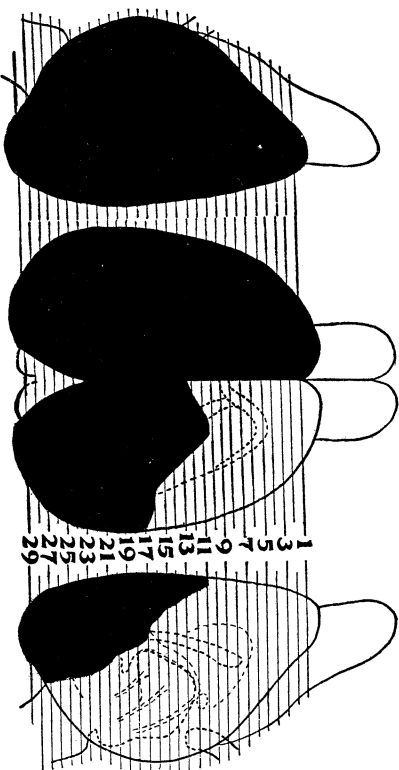

Fig. 14.—Extent of lesions in cases 34 and 35, with preservation of right motor and somesthetic areas only.
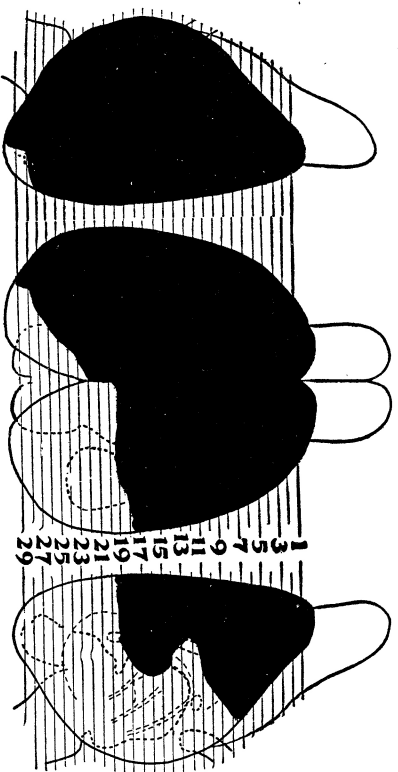

Fig. 15.—Extent of lesions in cases 32 and 36, with preservation of right visual and auditory areas only.

cases which made more than 75 errors in training (see Table I and diagrams of lesions), so that it is certain that the retardation shown by the animals of the series was not due to the destruction of any particular portion of the cerebral cortex.

The facts brought out in the foregoing analysis seem to

prove that the learning of Maze III may be retarded by injury to any of the cyto-architectural fields. The problem of the relative effects of lesions in different areas is complicated by the difference in size of the different fields and by the possible influence of the size of the lesion, irrespective of its locus. The average destruction of the cortex in the animals grouped according to locus of injury and suitable for this comparison ranges from 6.5 to 30.1 per cent of the entire neopallium. When the results are corrected for this difference in extent of lesion, there appears to be no significant difference between the effects of

TABLE VI

THE INFLUENCE OF REGIONAL DIFFERENCES IN THE POSITION OF THE LESION UPON THE LEARNING ON MAZE V.
ARRANGED AS IN TABLE V

Area	No. of Cases	Percentage of Destruction	Time (in Seconds)	Errors	Trials	Average Percentage Normal
$f, f', c, (i)$	4	22.2	2,287	66	22	244
$j, (p)$	2	18.2	2,300	65	14	206
$w, m, aa\ (p)$	5	24.1	9,079	374	60	987
w, m, aa, j	8	30.7	5,458	250	46	675
p	2	6.5	3,079	27	9	170
Transitional	6	24.7	5,029	219	42	616
Normal	15	0.0	1,365	26	7	100

DATA FOR MAZE IV

lesions within different areas. We may therefore conclude that equal injuries in different cortical areas produce equal amounts of retardation. Lesions to the transitional or primitive association (?) area are no more effective than lesions in other regions.

For Maze IV the data are less reliable, but there is indication of a distinct difference in their character (Table VI). The groups with injuries in the frontal areas require only twice as much practice as normals. Those with lesions overlapping the occipital fields, including the "transitional" group, require six or more times normal practice. The occipital groups have somewhat larger lesions than the others, but this difference is not great enough to account for the very great difference in the apparent effects of the lesions. This difference may be the result

of chance, but there is some justification for considering it significant. Maze IV, as used, stood in the middle of a small room lighted from one side and with the food box near a cabinet toward which the animals frequently reached and to which some of them jumped. Repeated tests showed that when the maze was rotated to any position a trained normal animal, placed on the middle of it, would make his way by the shortest route to the original position of the food box near the cabinet. All this suggests an element of pattern vision in this habit which would involve a greater activity of the occipital regions.

If this inference is correct, we must look upon the conditions of cerebral function in the learning of the open maze as differing from those in learning the inclosed maze. A general factor of some sort is indicated from the retardation after lesions in any of the areas, but an additional factor seems to enter when the lesion involves the visual areas and the problem of pattern vision.

DATA FOR BRIGHTNESS DISCRIMINATION

The results with brightness discrimination differ from those with either maze but are consistent with earlier studies of this habit. In two previous experiments I found that the rate of formation of the brightness habit was unaltered by the destruction of the entire area whose destruction subsequent to learning completely abolished the habit. Constants for the different cortical fields have been computed for this problem as for the mazes. For all areas the results approximate very closely to the normal average. Cases with destruction in the parietal and occipital regions (visual area) learned somewhat more readily than those with frontal and temporal injuries, but these differences correspond to the relative amounts of destruction in the different areas and to the involvement of lateral ventricles and thalamus.

Results from problems involving only brightness vision are to be distinguished sharply from those in which pattern vision is concerned, for they probably deal with a much more primitive or more generalized mechanism. For pattern vision, something like a point-for-point correspondence between retina and cortex seems essential, whereas nothing of the kind is required for sim-

ple discrimination of brightness. The available evidence indicates that the rate of learning of the simple brightness habit is independent of any part of the cerebral cortex, although the habit, when formed by normal animals, shows a definite cortical localization. I should anticipate quite different results in studies of pattern vision. The slow rate at which the rat forms habits involving pattern vision has thus far prevented any adequate study of such habits.

THE DOUBLE-PLATFORM BOX

In an earlier study (Lashley, 1917) it was found that no lesion up to 50 per cent of the cerebral cortex produced any serious retardation in the rate of formation of the habit of opening the latch box shown in Figure 1. Review of these experiments reveals that the lack of effect was equally apparent for all of the areas of the cortex. When the habit is formed in normal animals, it shows definite localization in the frontal region (Hunter, 1926), yet its rate of formation is independent of any particular part of the cortex. In these respects it parallels exactly the conditions found for the habit of brightness discrimination.

CONCLUSIONS

The data on these four problems suggest three diverse types of influence upon learning, arising from brain injuries. First, for some problems, a retardation results from injury to any part of the cortex, and for equal amounts of destruction the retardation is approximately the same. The magnitude of the injury is important; the locus is not. Second, there may be a general retardation, arising from any injury, to which is added a specific retardation resulting perhaps from sensory deficiency and associated with lesion to a particular cortical field. Third, for still other habits there may be a complete absence of any effect upon learning from lesions of any extent or of any locus, within the wide limits of these experiments. The second of these types, based upon Maze IV, is no more than suggested by the results of these experiments but seems pretty well established by much clinical work with man. The first and third are clearly established in these experiments.

The results of the study of regional differences in the position of the lesions raises the question of qualitative differences in the effects. Admitted that lesions to any part of the cortex produce retardation, is the mechanism in all cases the same, or is the retardation for each locus the result of a different set of factors? The latter seems the more probable; and one naturally thinks of sensory defects or cerebral anesthesias, varying with the region injured, as the most likely cause of the retardation.

TABLE VII

CORRELATIONS (RANK ORDER) BETWEEN THE PERCENTAGE DESTRUCTION OF THE CEREBRAL CORTEX AND THE AMOUNT OF PRACTICE REQUIRED FOR LEARNING THE VARIOUS PROBLEMS, AS MEASURED BY DIFFERENT CRITERIA

	Time (in Seconds)	Errors	Trials	Average
Maze III..........	0.615±0.072	0.857±0.031	0.768±0.047	0.75
Maze II...........	0.515±0.089	0.650±0.070	0.568±0.082	0.58
Maze I............	0.191±0.167	0.299±0.159	0.164±0.169	0.20
Brightness discrimination....	0.339±0.133	0.503±0.108	0.406±0.121	0.45
Retention, Maze III...	0.339±0.133	0.508±0.111	0.556±0.104	0.46
Retention, Maze I.....	0.023±0.137	0.002±0.138	−0.079±0.137	−0.02
Reversal, Maze I......	0.395±0.124	0.427±0.119	0.309±0.134	0.38
Maze IV...........	0.380±0.121	0.679±0.077	0.586±0.093	0.55

THE RELATION BETWEEN THE DEGREE OF DETERIORATION AND THE EXTENT OF INJURY

The interpretation of the sensory control of the maze habit is complicated and difficult. The problem enters into all phases of our experiments, which in turn contribute to the interpretation of the sensory problem. We must therefore leave its discussion until the question can be considered in relation to the whole available evidence.

The range in extent of the lesions in the series of operated animals was from 1.5 to 81.2 per cent of the total surface area of the cerebrum, with an average of 31.1 per cent. Correlations between the magnitude of the injury and the amount of practice required for learning have been computed for the various criteria of learning for the chief problems included in this study. They are given in Table VII. With one exception, retention of Maze I,

the correlations are positive and in most cases in excess of three times their probable errors. They show clearly that for most of the problems there is some relationship between the extent of injury and the amount of practice necessary for learning. Is this a true functional relationship, or is it a spurious result of some factor other than the actual elimination of tissue?

POSSIBLE CAUSES OF SPURIOUS CORRELATION

A spurious correlation might arise from any one of the following conditions:

1. The severity of operative shock might be proportional to the amount of destruction of tissue or to the amount of tissue destroyed. Thus, recovery from the operation might be delayed in cases with extensive destruction and so retard their learning. This might account for the correlations in the problem used immediately following operation, but will not account for the correlation in Maze IV, where training of the severely injured cases was begun 4 months or more after operation. It is also inconsistent with the fact that the correlation for Maze IV is as high as that for Maze II and higher than that for Maze I, although both the latter problems were used much sooner after operation.

2. If learning were conditioned by the intactness of a single insular association area, a greater percentage of large than of small lesions would invade this area by chance and retardation would occur more frequently among animals with large lesions than among those with small. In the discussion of the retardation from lesions in different areas, it has been shown that the injuries in quite different parts of the cortex are equally effective in producing retardation and that no common area is involved in all retarded cases. Moreover, inspection of Table XI and Figure 9 shows that the correlation is not due to inclusion of different proportions of retarded and unretarded cases in different parts of the range. The deviations in amount of practice form a continuous series, as does the percentage of destruction.

3. A similar argument might be advanced with respect to the invasion of subcortical nuclei. The more extensive cortical lesions are attended by injuries to the thalamus and other struc-

tures which may be the important centers for learning. I have corrected for this possibility in the case of the thalamus. Eleven of the 37 cases showed some injury to the thalamus, for the most part very slight, but in a few cases quite extensive. Correlations for Maze III were computed separately for the 26 cases without thalamic lesions and for the 11 with such injuries. They were the following:

For all cases, $p = 0.86$ for errors
For cases without thalamic lesion, $p = 0.83$ for errors
For cases with thalamic lesions, $p = 0.86$ for errors

The omission of the thalamic cases thus reduces the correlation only from 0.86 to 0.83, and there is no reason to believe that the striatum, septum, or hippocampal structures are more intimately concerned with maze learning than is the thalamus, and so we cannot ascribe the correlation to injury to subcortical structures.[1]

It seemed, on the other hand, that failure to take the subcortical lesions into consideration might have resulted in a lesser correlation than actually exists between neural mass and rate of learning, since measurement of the surface area does not express the full extent of injury. I have attempted to correct for this in the following way:

The lesions to subcortical structures for each case are shown in Table VIII. A number was assigned to each structure, a purely arbitrary estimate of its relative importance, determined chiefly by its relation to projection tracts. These numbers were: septum, 1; striatum, 2; fornix, 1; hippocampus, 1; superior colliculus, 1; thalamus, 3. For striatum, hippocampus, and thalamus the lesions were recorded as of three grades: slight, medium, and extensive; others as of one grade only. The sum of the products of structure number by grade of injury gave an index number for each animal. Thus an animal with injury to the septum, nucleus habenula, superior colliculus, and dorsal halves of both hippocampi received the total score of 7. The animals were assigned numbers corresponding to their rank order on the basis

[1] This is not true for the habit of brightness discrimination, as will be brought out later.

of surface injury. To these numbers the indices of subcortical injury were added, and on the basis of the sums a new rank order

TABLE VIII

Record of the Subcortical Lesions for All Cases Included in Table I

No.	Thalamus	Striatum	Superior Colliculus	Hippocampus	Septum
1					
2					
3					
4					
5					
6					
7					
8					
9					
10				1	
11		1 (?)		1	
12				1	
13				2	
14		1		1	
15					
16				2	
17				1	
18				1	
19					
20	1		3	2	
21	1		1		
22					
23				1	
24		2	1	2	
25				2	
26			1	1	
27	1			1	1
28	1			1	
29	1	1		2	1
30	1		1	2	1
31	3	2		2	
32		2	1	2	
33	3	2	1	3	
34	1	2	1	1	
35	3	2		3	
36	3	3	1	3	
37	1	2		2	

was determined and correlated with the training records. This gave for Maze III the following coefficients:

Time, $p = 0.672$,
Errors, $p = 0.874$,
Trials, $p = 0.800$,

which represent an increase in all coefficients of about 3 per cent over those obtained by consideration of the superficial lesions only. No dependence can be placed on these as absolute values, but they serve to show that if lesions to internal structures could be accurately evaluated the method would most probably reveal a still closer correspondence between learning ability and amount of functional tissue than is shown by computing surface lesions only.

4. If retardation were due solely to the destruction of a critical amount of tissue, the inclusion of animals with injuries both above and below this quantity might result in some correlation. Table XI (page 73) shows, for the four mazes, the average amount of practice required by animals with different amounts of destruction. For Maze I there is a pronounced increase in the amount of practice required when the lesion exceeds 20 per cent; for Mazes II and III, when it exceeds 10 per cent. No such sudden increment appears with Maze IV. But above this critical point for each of the mazes the increase in practice follows the increase in extent of lesion, so that there can be no doubt that the amount of practice is a continuous function of the extent of injury.

This seems to exhaust the possible sources of spurious correlation. None of the four is adequate to account for the relationships found for the maze habits, and the conclusion seems justified that the retardation in learning is a true function of the extent of injury to the cerebrum.

ANALYSIS OF THE CORRELATIONS

Turning now to a comparison of the correlations between lesion and practice shown in the different problems (Table VII), we find a range from a high positive to a slight negative. The maximum correlation was given by Maze III. The distribution of cases for extent of lesion and errors in training is shown in Figure 16. The correlation is obviously continuous throughout the greater part of the range. The correlations for this problem are 0.61 for time, 0.86 for errors, and 0.77 for trials; are remarkably high, and are significantly greater than their probable errors.

The correlations for the other mazes are less reliable than those for Maze III, and their lesser magnitude presents some difficulty of interpretation. If brain injuries act uniformly, we should expect to find the same correlation for all the mazes, even though a relatively smaller retardation were produced by a given extent of lesion in one than in another. That is, the regression of practice on extent of destruction should be less where the absolute retardation is less, but the relative influence of different
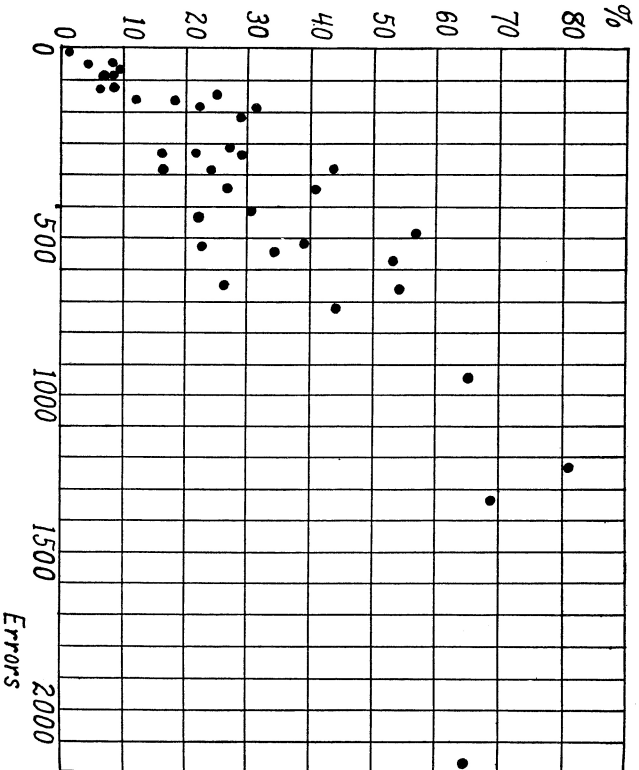

FIG. 16.—Distribution of extent of injury and errors in learning Maze III. Ordinates represent percentage of neopallium destroyed; abscissae, number of errors made during training.

amounts of injury should remain the same. It must be remembered, however, that the rate of formation of the maze habit is subject to many chance influences and that the smaller the absolute effect produced by any agent the greater is the likelihood that the effect will be concealed by chance factors, and consequently the smaller will be any correlation which depends upon the isolation of the effects of the single agent. Table IX compares the magnitude of the correlations for errors and lesions

with the range of variation in errors for the different problems. The correlations follow roughly the amount of variation in the rate of learning and so bear out the conclusion that the lower correlations are due to the unreliability of the simpler mazes for the detection of slight individual differences.

From this it seems just to conclude that the correlation for Maze III represents most truly the relationship between the magnitude of lesion and the degree of retardation in learning. We have seen, from the consideration of the possible causes of

TABLE IX

COMPARISON OF THE MAGNITUDE OF THE CORRELATIONS BETWEEN EXTENT OF CEREBRAL DESTRUCTION AND RETARDATION IN LEARNING WITH THE RANGE OF VARIATION IN ERRORS FOR EACH OF THE PROBLEMS STUDIED

	Average Correlation	Range of Variation in Errors
Maze III	0.75	2,282
Maze II	0.58	632
Maze IV	0.55	766
Retention, Maze III	0.46	578
Brightness discrimination	0.45	98
Reversal, Maze I	0.38	48
Maze I, learning	0.20	91
Retention, Maze I	0.02	50

spurious correlation, that the constants obtained represent a real and continuous relation between the amount of destruction and the difficulty in learning. Since shock seems to be eliminated by the comparison of results with Mazes III and IV, it seems necessary to conclude that the rate of learning is dependent upon the amount of cerebral tissue which remains intact and capable of functioning. Where the range in the total amount of tissue is very great, as in these experiments, and where the learning capacity is not obscured by chance factors, as with Maze III, the correspondence is so close as to suggest that learning of this sort is a direct function of the quantity of tissue.

CORRELATIONS WITHIN SEPARATE CORTICAL FIELDS

We have next to inquire whether this quantitative relationship holds for all parts of the cortex or only within restricted

areas. The correlations between extent of injury and number of errors made in training have been computed separately for Mazes III and IV for each of the principle histological areas listed in Tables V and VI. The constants obtained are shown in Table X. They range from 0.55 to 0.90, and the majority are above 0.70. The number of cases in each group is too small to give reliability to the coefficients, but all are positive and surprisingly uniform for such small samples. Considered as a whole, they give clear evidence that within each of the cyto-architectur-

TABLE X

CORRELATIONS BETWEEN EXTENT OF CEREBRAL LESION AND NUMBER OF ERRORS MADE IN TRAINING IN MAZES III AND IV, WITHIN SEPARATE GROUPS OF ANIMALS HAVING LESIONS CONFINED LARGELY TO SINGLE HISTOLOGICAL DIVISIONS OF THE CORTEX

	Motor	Somesthetic	Visual	Visuo-somesthetic	Transitional
Maze III:					
p for errors......	0.90	0.80	0.73	0.68	0.78
Number of cases....	5	4	7	10	7
Maze IV:					
p for errors........	0.90	0.60	0.55	....	....
Number of cases....	5	6	9	....	....

al fields the degree of retardation in learning produced by brain injury is proportional to the magnitude of the injury. We have seen from the data presented in the preceding section that retardation is produced by a lesion in any of the cortical fields and that diverse lesions of equal magnitude produce, on the average, equal effects. The approximately equal correlations within the single fields further show that the retardation is dependent solely upon the extent of destruction, irrespective of its locus within the cerebral hemispheres. For learning of the mazes no part of the cortex is more important than any other. This would seem to imply, as a corollary, that in maze learning the functions of the different cerebral areas are qualitatively the same. This would follow certainly if an exact quantitative equivalence of different parts were shown, but the correlations are not reliable enough to establish such an exact relationship. Further discussion of this question must be postponed until data on the sensory components of the maze habit have been presented.

CORRELATIONS FOR THE HABIT OF BRIGHTNESS DISCRIMINATION

The average correlation of $p=0.45$ for the brightness habit is puzzling. Animals with brain lesions are, on the average, slightly superior to normals in the formation of this habit, yet the greater the lesion the less readily they learn. Fortunately data are available for a check upon this result. In a previous study of the formation of this habit after occipital lesions (1927), I found a correlation of only $p=0.11\pm0.14$ between extent of injury and amount of practice for learning. In that series the maximum destruction was 43 per cent of the cortex. If we exclude all cases of the present series with more than this amount of destruction, the correlation for the remaining cases falls to $p=0.11\pm0.17$, indicating that the larger correlation is due to the inclusion of the cases with the more extensive lesions. Among these latter were several with injury to the visual nuclei of the thalamus. If we omit the cases with evident lesion to the visual thalamic nuclei, the correlation is reduced from $p=0.45$ to $p=0.22$. A similar omission in computing the correlations for Maze III results in a reduction of only 2 per cent in the coefficient for that function. Thus it appears that the greater part of the correlation for the brightness habit is the result of the inclusion of cases with thalamic injuries and that this factor does not contribute in equal degree to the correlations for the mazes.

There is evidence from other sources that injuries to the optic radiations or lateral geniculate bodies retard the formation of the visual habit, and we may safely conclude that the apparent dependence of this habit upon the extent of cortical lesion is largely the result of the inclusion of cases with thalamic injuries.

However, this does not clear up the whole problem. There remains the apparent superiority of operated over normal animals in the learning of brightness discrimination. Herrick (1926, pp. 205-9) has discussed this question in some detail. He concludes, "The presence of uninjured cerebral cortex may actually retard learning a very simple habit by reason of the complication of the processes through intercurrent cortical associations from other sensory fields." A parallel case is perhaps the reader as-

sorting of weights in the Binet tests by children than by adults. However, the superiority of the operated animals in the visual problem is slight and may well be due to chance.

CEREBRAL FUNCTION AS CONDITIONED BY THE COMPLEXITY OF THE PROBLEM

Three of the problems used, Mazes I, II, and III, involve, in so far as one can determine, the same kind of sensory and motor processes. They differ in the length of the true path, in the number of turns to be made, and in the relative position of the turns, but present strictly comparable sensory situations. Maze IV differs from these three both in the intensity of motivation (restriction of activity to a narrow and somewhat unsteady path) and in the sensory cues which it presents. Although its objective complexity is the same as that of Maze III, normal animals required less than half as much practice to learn it as to learn the corresponding inclosed maze. Although I have included the records from it in the following tables, it must be borne in mind that it is not strictly comparable to the other three.

The three inclosed mazes present respectively one, three, and eight culs-de-sac to be avoided. This gives no measure of their actual difficulty, which can be determined only empirically. For normal animals the average numbers of errors made in learning the three mazes were the following: Maze III, 47.4; Maze II, 16.2; and Maze I, 7.3. This gives a ratio of relative difficulty for the three of 6.5:2.2:1. The mazes were used in the order, III, II, I, which means that positive transfer, due to adaptation to handling and the like, must favor the simpler mazes and tend to reduce the relative amount of practice required for learning them. In spite of this, relatively less practice is required by normal animals for the complex mazes than for the simpler.

For comparisons of the records of operated animals, a complication is introduced by the fact that not all of the animals reached the criterion of 10 successive errorless trials within the limits of the experiment, and that training was discontinued after an arbitrarily limited amount of practice. An attempt was made to set a limit for each maze proportionate to the average

trials required by normal animals, but, as it turned out, the limits set for the simpler mazes were relatively too low. The number of trials at which training was terminated, with its ratio to the normal average for learning, is given below:

	Maze III	Maze II	Maze I
Trials	150	100	60
Ratio to normal	7.5:1	6.0:1	4.0:1

Eleven animals failed Maze III; 3 failed Maze II; and 6, Maze I. Thus, if we include all cases, we may exaggerate the practice required for Maze III, since 150 trials on this maze represents a relatively worse record than 60 trials on Maze I. On the other hand, if we exclude all cases which did not finish, we throw out more of the poorer records for Maze III and so decrease its apparent difficulty in relation to the others.

However, the majority of errors are made during the early trials, and, by basing our comparison upon errors, we avoid much of this difficulty. The errors made by all animals in the three mazes were the following:

	Maze III	Maze II	Maze I
Average errors, all cases	460.0	77.8	22.3
Ratio on Maze I	20.6	3.5	1

Excluding those animals which failed to reach the criterion of learning we find:

	Maze III	Maze II	Maze I
Average errors, all cases which learned	306.8	52.0	14.9
Ratio on Maze I	20.6	3.5	1

The relative amounts of practice, measured in errors, required for learning the three mazes are thus exactly the same, whether we include or exclude the cases which failed to reach the criterion in the allotted time. The following discussion is therefore based upon the error records of all animals.

The simpler problem offers difficulties which are not much greater for animals with brain lesions than for normal ones; and, correspondingly, the difficulty does not greatly increase with increasing magnitude of brain injury. The more complex problem,
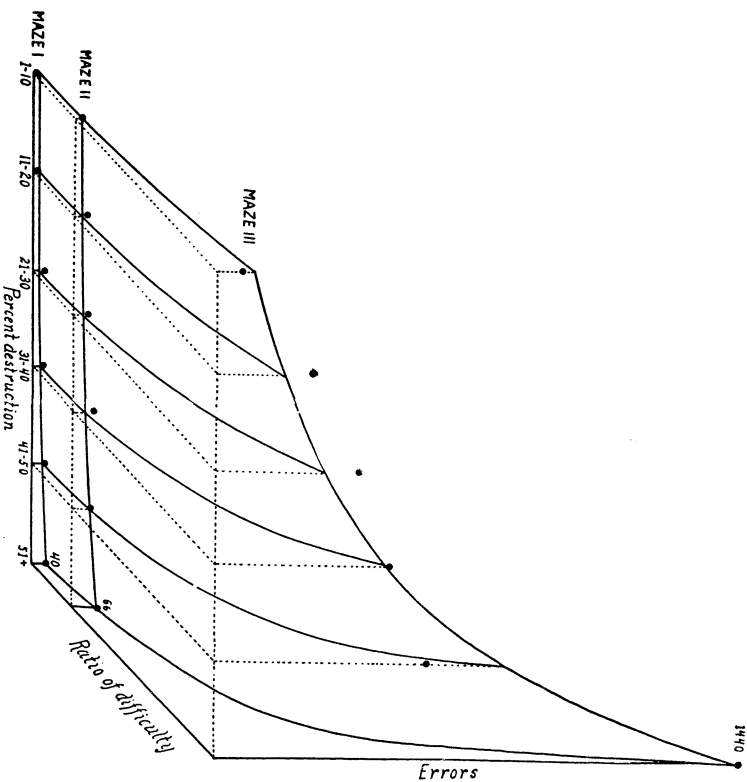

Fig. 17.—The relation between the extent of cerebral lesion, difficulty of the problem to be learned, and degree of retardation. The separation of the curves represents the relative difficulty of the problems for normal animals; the abscissae of the curves, the percentage destruction; and the ordinates, the number of errors made during training.

on the other hand, is more difficult for animals with lesions than for normals; and as the magnitude of the lesion increases, the difficulty of the problem becomes progressively greater.[2]

[2] This is borne out by the results of Cameron (1928) on maze learning after frontal lesions. He used a maze more complicated than any included in my study, and found a marked reduction of learning ability after smaller lesions than were effective in my cases.

The results with the habit of brightness discrimination do not seem to be in harmony with this conclusion, nor are those with the double-platform box reported earlier (Lashley, 1920). In the learning of both of these problems the operated animals, even with very extensive cerebral lesions, gave no indication of retardation. Yet, measured in terms of practice required for learning by normal animals, these two problems are very much more difficult than are any of the mazes. The average for normal animals on the double-platform box is 142 ± 9 trials; and for the brightness habit, 135 ± 12. The most difficult of the mazes required only 19 trials for normal animals. Thus the two problems on the learning of which cerebral injury had no effect seem to be very much more difficult than the mazes.

This apparent inconsistency in the results with the different problems may be due to any of a number of factors. We have seen that it cannot be ascribed to differences in the incentives used, but there remain possibilities of differences in the sensory or motor components involved in the habits. It may also be that the unaffected habits are psychologically more simple than the maze habits, even though the practice required by normal animals is greater. Discussion of this must be postponed until the experiments bearing upon the sensory requirements of the maze have been considered.