6-5-1937

# The Relative Influence of the Locus and Mass of Destruction Upon the Control of Handedness by the Cerebral Cortex

La Charles Fracarol

FRA-
CAROL

CON-
TROL
OF
HANDED
NESS

# THE RELATIVE INFLUENCE OF THE LOCUS AND MASS OF DESTRUCTION UPON THE CONTROL OF HANDEDNESS BY THE CEREBRAL CORTEX

By

La Charles Fracarol

A Thesis
Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Arts in Psychology

University of New Mexico

1937

This thesis, directed and approved by the candidate's committee, has been accepted by the Graduate Committee of the University of New Mexico in partial fulfillment of the requirements for the degree of

MASTER OF ARTS

George P. Hammond
DEAN

June 5, 1937
DATE

Thesis committee

Geo. M. Peterson
CHAIRMAN

B. F. Haught

F. W. Allen

ACKNOWLEDGMENT

The writer wishes to express her gratitude to Dr. George M. Peterson for suggesting the problem undertaken in this study, for performing the brain operations, and for his helpful criticisms and suggestions throughout the prosecution of the study.

[illegible]

The [illegible]
Degree [illegible]
in this study, [illegible]
for his helpful [illegible]
prosecution of this study.

TABLE OF CONTENTS

## LIST OF TABLES

LIST OF TABLES

TABLE PAGE

# CHAPTER I

## INTRODUCTION

## REVIEW OF THE LITERATURE

The doctrine of localization of function in the cerebral cortex has raised a number of interesting questions which can be answered satisfactorily only by further research. Not only is there the question of the relative loci of various functions, but also, the type of functions that have been localized, the conditions which bring about this specialization, the degree to which the specialization has occurred within a local area, the influence of adjacent regions in producing faciliatations or inhibitions, individual variations and so on. The doctrine has been criticized in recent years mainly for its failure to give an adequate account of the so called higher mental processes. Yet even here, a more careful analysis based on increasingly refined techniques has given some substantiation to certain aspects of the doctrine.

Lashley, working on the visual brightness habit has turned in three separate reports, parts of which have led to somewhat diametrically opposed conceptions. The first study pointed to the occipital cortex as the crucial area for brightness discrimination, although animals could acquire

[illegible]

CHAPTER I

INTRODUCTION

[illegible]

The occurrence of [illegible] in [illegible] general [illegible] which one [illegible] search. [illegible] of various [illegible] have been [illegible] specialized [illegible] occurred [illegible] gions [illegible] variations [illegible] recent years [illegible] count of [illegible] here, [illegible] techniques [illegible] of the [illegible].

[illegible]

the habit as readily without this area. However, no one part of the occipital region appeared more important than another, and the concept of equipotentiality was accordingly suggested.[1]

A reanalysis of the brightness habit followed the discovery that a local area within the occipital cortex was necessary for detailed vision. The reanalysis now revealed that the destruction of this area interfered with the retention of the brightness habit, but that adjacent regions contributed to the degree of loss in approximate proportion to the extent of their destruction.[2]

More recently, improved staining techniques have resulted in the tracing of fibre tracts from retina to cortex through the lateral geniculate nucleus and have given a very close correspondence of parts. Based on this knowledge a third study of the control of the brightness habit by the cortex revealed a high degree of localization. Partial losses in the habit (presumably) resulting from

---

[1] Karl S. Lashley, "Studies of Cerebral Function in Learning. VII. The Relation Between Cerebral Mass, Learning, and Retention," Journal of Comparative Neurology, 41: 1-58, 1926.

[2] Karl S. Lashley, "Studies of Cerebral Function in Learning. VIII. A Reanalysis of Data on Mass Action in the Cerebral Cortex," Journal of Comparative Neurology, 54: 80-81, February, 1932

the [illegible] rapidly without [illegible]. However, no [illegible] part of the cerebral [illegible] [illegible] [illegible] the cortex, and the concept of [illegible] [illegible] [illegible] suggested.[1]

A [illegible] of the [illegible] [illegible] the discovery that a local area [illegible] [illegible] necessary for detailed [illegible] [illegible] that the destruction of [illegible] [illegible] [illegible] of [illegible] [illegible] [illegible] contributed to [illegible] [illegible] to the [illegible] [illegible].

[illegible], [illegible] [illegible] [illegible] in the [illegible] of [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] a very close [illegible] of [illegible]. [illegible] [illegible] a [illegible] [illegible] of the [illegible] of [illegible] by the [illegible] [illegible] a [illegible] [illegible] of [illegible].

Partial losses in the [illegible] (previously) [illegible] [illegible]

---

[1] Karl S. Lashley, "Studies of Cerebral Function in Learning. VII. The Relation [illegible] [illegible]," Journal of Comparative Neurology, [illegible], 1926.

[illegible] S. Lashley, "Studies of Cerebral Function in Learning. VIII. [illegible] [illegible] [illegible]," Journal of Comparative Neurology, [illegible] February, [illegible] destructions outside the critical area were really found to be due to amblyopic disturbances which wide-spread destructions have a greater chance of producing.[3] Thus, as a result of refinement in techniques, the localization theory is in good standing once more in the analysis of visual habits. Nevertheless, there are other habits, noticeably the maze and latch boxes which have not been so successfully analyzed, and the question can be raised as to what part some of the alternative concepts to localization play in types of performance other than sensory discrimination.

Bartley[4] suggested that the concept of physiological gradients might replace the doctrine of localization, and Peterson[5] applying it in his study of the cerebral mechanisms of handedness concluded that the gradient hypotheses would not account for the facts "without making further assumptions." However, his crucial analysis involved ambidextrous rats, only two of which were suitable for the

---

[3] Karl S. Lashley, "The Mechanism of Vision. XII. Nervous Structures Concerned in the Acquisition and Retention of Habits Based on Reactions to Light," Comparative Psychology Monographs, No. 2, 11: 60, February, 1935.

[4] S. H. Bartley, "Gross Differential Activity of the Dog's Cortex as Revealed by Action Currents," Psychology Monographs, 44: 30-56, 1933.

[5] George M. Peterson, "Mechanisms of Handedness in the Rat," Comparative Psychology Monographs, No. 6, 9: 36-39, April, 1934.

destructions outside the critical area were generally found to be due to [illegible] disturbances [illegible] the after-effects of operation have a greater degree of [illegible].[3] Thus, as a result of refinement in technique, the localization theory is in good standing once more in the analysis of visual habits. Nevertheless, there are other habits, especially the maze and latch boxes, which have not been so successfully analyzed, and the question can be raised as to what part one of the alternative concepts to localization play in types of performance other than sensory discrimination.

Gerard[4] suggested that some pattern of [illegible] gradients might replace the concept of localization, and Sperry[5] used [illegible] it in his study of the [illegible] mechanisms of [illegible] yet the [illegible] hypotheses [illegible] for the [illegible] further assumptions. [illegible], however, his [illegible] individually [illegible] independent [illegible], only two of which were [illegible] for the

---

[3] Karl S. Lashley, "The Mechanism of Vision. XVII. [illegible] of Rat's [illegible]," Comparative Psychology Monographs, No. [illegible], 11: [illegible].

[4] R. W. Gerard, "[illegible]," [illegible].

[5] [illegible], "[illegible] of [illegible]," [illegible], 20-38, April, [illegible].

problem at issue, and only one of which was an exception to the hypothesis being tested. The present research was organized around this problem and is really an extension of the number of cases studied by Peterson.

## THE PROBLEM

<u>Statement of the problem</u>. Specifically, this experiment sought an answer to the following questions:

(1) Is there evidence for a critical area in the cerebral cortex for the control of handedness, and if so, what are the limits of this area, i.e., what is the least destruction within this region that will produce transfers in handedness?

(2) Will a destruction outside of the critical area have an effect, and if so, how large must such a destruction be to cause it?

(3) What bearing will the results have upon current theories of cerebral functioning, including localization of function, physiological gradients, mass action, and equipotentiality?

## PROCEDURE

<u>Observational methods</u>. Ambidextrous rats were used, since these are assumed to be more delicately balanced, and

[illegible], and [illegible] of [illegible] to [illegible] to the [illegible] basis. [illegible] each paragraph [illegible] and [illegible] the [illegible] of [illegible] to [illegible].

THE PROBLEM

__Statement of the Problem.__ [illegible] the experiment sought to answer the following questions:

(1) Is there evidence for a [illegible] in the [illegible] with [illegible] of [illegible], and [illegible] when [illegible] the [illegible] of [illegible] [illegible] within this region [illegible] with [illegible] in [illegible]?

(2) [illegible]

(3) [illegible] the [illegible] of [illegible], [illegible] of [illegible], [illegible] and [illegible]?

PROCEDURE

[illegible]

thus show transfer effects from minor disturbances which might be ineffective in strongly right or left handed rats. Altogether, twenty-nine ambidextrous cases were used in this study, necessitating the observation of more than 300 animals, since only about ten per cent of unselected rats are ambidextrous.

Handedness was determined by the use of Peterson's food situation, a record being kept of the number of times each hand was used until a total of fifty reaches were taken. Several animals were observed for a longer period as a check to determine whether fifty reaches gave a fair sampling of the animals preferential handedness. Their records in intervals of fifty reaches are given in Table I. It will be seen that the first fifty reaches give an indication of the animals' ambidexterity. In every case where fifty reaches were taken, ambidexterity is revealed during the first fifty reaches and continues to be shown during successive groups of fifty reaches. However, the degree of ambidexterity shows considerable fluctuation, indicating that not too much reliance can be placed upon the percentage of time one hand is used.

The animals were observed for handedness on at least seven occasions before the operation. Some animals were observed for a longer period of time, and in two instances the animals were observed seventy-two times over a period of

TABLE I

RECORDS SHOWING THE RELIABILITY OF FIFTY HAND REACHES IN INDICATING AMBIDEXTERITY

| Observation period | Rat No. 11 ♀ | | Rat No. 13 ♀ | | Rat No. 17 ♂ | | Rat No. 24 ♂ | | Rat No. 29 ♂ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 3 | 47 | 32 | 18 | 12 | 38 | 44 | 6 | 21 | 29 |
| | 17 | 33 | 31 | 19 | 23 | 27 | 46 | 4 | 20 | 30 |
| | 11 | 4 | 10 | 20 | 29 | 21 | 38 | 12 | 13 | 37 |
| | | | | | 18 | 13 | 9 | 1 | 4 | 14 |
| 2 | 16 | 34 | 28 | 22 | 16 | 34 | 48 | 2 | 29 | 21 |
| | 4 | 46 | 34 | 16 | 16 | 34 | 47 | 3 | 22 | 28 |
| | 3 | 35 | 10 | 9 | 21 | 29 | 49 | 1 | 17 | 33 |
| | | | | | 17 | 7 | | | 6 | 5 |
| 3 | | | | | 14 | 36 | 45 | 5 | 11 | 39 |
| | | | | | 30 | 20 | 45 | 5 | 14 | 36 |
| | | | | | 34 | 16 | 46 | 0 | 21 | 29 |
| | | | | | 7 | 0 | | | 13 | 19 |
| 4 | | | | | 19 | 31 | | | 12 | 38 |
| | | | | | 24 | 26 | | | 3 | 47 |
| | | | | | 16 | 15 | | | 10 | 40 |
| 5 | | | | | 21 | 29 | | | 2 | 48 |
| | | | | | 26 | 24 | | | 2 | 48 |

274 days (Nos. 1 and 2). These two cases were observed for this extended period to discover if the period selected, seven days, was sufficiently long to give a reliable index of the animals' ambidexterity. The results of these two cases are shown in Table II. It will be noted that both animals fluctuated gradually from extreme handedness to ambidexterity, and from ambidexterity to the opposite extreme. These periods of fluctuation ranged from seven days to 219 days. However, in 97 per cent of the days they were ambidextrous rather than single handed, and in no case was the single handedness shown for more than two successive days. Fluctuations of this sort are encountered in cases that are definitely ambidextrous, while animals with stronger preferences for one hand fail to reveal such striking fluctuations. From these results it would appear that observation taken over a period of seven days are a good indication of the extent of ambidexterity of rats. It occasionally happens that an animal exhibits an early ambidexterity which is soon overcome, whereupon he remains single handed. Rat No. 24 is such an example, as a reference to his record in the Appendix will reveal. However, such cases always manifest these preferences relatively early, and none have been known to show it after an extended period of consistent

# TABLE II

## RECORDS ON THE HANDEDNESS CONSISTENCY OF AMBIDEXTROUS RATS

| Observation Period | Rat No.1 ♀ | | Rat No.2 ♀ | | Observation Period | Rat No.1 ♀ | | Rat No.2 ♀ | |
|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | | Right | Left | Right | Left |
| 1 | 0 | 50 | 43 | 7 | 39 | 32 | 18 | 48 | 2 |
| 2 | | | 49 | 1 | 40 | 23 | 27 | 50 | 0 |
| 3 | | | | | 41 | 28 | 22 | 49 | 1 |
| 4 | 28 | 22 | 34 | 16 | 42 | 34 | 16 | 49 | 1 |
| 5 | 6 | 44 | 41 | 9 | 43 | 27 | 23 | 46 | 4 |
| 6 | | | 34 | 16 | 44 | 29 | 21 | 37 | 13 |
| 7 | 13 | 37 | 44 | 6 | 45 | 32 | 18 | 24 | 26 |
| 8 | 18 | 32 | 49 | 1 | 46 | 27 | 23 | 45 | 5 |
| 9 | 24 | 26 | 49 | 1 | 47 | 20 | 30 | 48 | 2 |
| 10 | 9 | 41 | 48 | 2 | 48 | 30 | 20 | 50 | 0 |
| 11 | 28 | 22 | 44 | 6 | 49 | 7 | 43 | 50 | 0 |
| 12 | | | 34 | 16 | 50 | 21 | 29 | 49 | 1 |
| 13 | 40 | 10 | 38 | 12 | 51 | 24 | 26 | 41 | 9 |
| 14 | 27 | 23 | 29 | 21 | 52 | 11 | 39 | 28 | 22 |
| 15 | 16 | 34 | 28 | 22 | 53 | 19 | 31 | 47 | 3 |
| 16 | 15 | 35 | 19 | 31 | 54 | 28 | 22 | 50 | 0 |
| 17 | | | 8 | 42 | 55 | 21 | 29 | 27 | 23 |
| 18 | 32 | 18 | 29 | 21 | 56 | | | 13 | 37 |
| 19 | 27 | 23 | 16 | 34 | 57 | 42 | 8 | 22 | 28 |
| 20 | 39 | 11 | 0 | 50 | 58 | 33 | 17 | 1 | 49 |
| 21 | | | 14 | 36 | 59 | 36 | 14 | 44 | 6 |
| 22 | 10 | 40 | 8 | 42 | 60 | 24 | 26 | 48 | 2 |
| 23 | 37 | 13 | 11 | 39 | 61 | 26 | 24 | 32 | 18 |
| 24 | 39 | 11 | 6 | 44 | 62 | 28 | 22 | 39 | 11 |
| 25 | 36 | 14 | 10 | 40 | 63 | 15 | 35 | 19 | 31 |
| 26 | 31 | 19 | 44 | 6 | 64 | 30 | 20 | 24 | 26 |
| 27 | 34 | 16 | 44 | 6 | 65 | 35 | 15 | 15 | 35 |
| 28 | 21 | 29 | 50 | 0 | 66 | 30 | 20 | 30 | 20 |
| 29 | 44 | 6 | 47 | 3 | 67 | 14 | 36 | 24 | 26 |
| 30 | 50 | 0 | 44 | 6 | 68 | 10 | 40 | 14 | 36 |
| 31 | 29 | 21 | 44 | 6 | 69 | 4 | 46 | 3 | 47 |
| 32 | 18 | 32 | 44 | 6 | 70 | 0 | 50 | 0 | 50 |
| 33 | 32 | 18 | 17 | 33 | 71 | 0 | 50 | 6 | 44 |
| 34 | 30 | 20 | 25 | 25 | 72 | 10 | 40 | 16 | 34 |
| 35 | 10 | 40 | 14 | 36 | 73 | 13 | 37 | 9 | 41 |
| 36 | 20 | 30 | 10 | 40 | 74 | 25 | 25 | 14 | 36 |
| 37 | 24 | 26 | 21 | 29 | | | | | |
| 38 | 8 | 42 | 19 | 31 | | | | | |

ambidexterity.[6]

Operational techniques. All operations were unilateral and were performed under deep ether anaesthesia. Ethyl alcohol was used as an antiseptic since it is known that this chemical does not leave permanent functional effects.[7] A one eighth inch or a one fourth inch trephine was used to open the skull for the large destructions. In a few of the small destructions a 5 mm drill was used since it made a sufficiently large opening to admit one wire of the cautery. Destructions in all cases were made with the thermocautery. In cases with the small drill opening only one wire could be inserted through the hole. The cautery was allowed to reach a red heat and then inserted twice to a depth of about one eighth inch. Seven days were allowed for the animals to recover from the operation, whereupon they were reobserved for another period consisting of at least seven successive days, and thereafter once per week until two months had elapsed. Many more observations were taken in instances where the records were

---

6 George M. Peterson, "Mechanisms of Handedness in the Rat", *Comparative Psychology Monographs*, No. 6, 9: 2-3, April, 1934.

7 George M. Peterson and Genevieve W. Carter, "The Local Application of Drugs to the Motor Cortex of the Rat," *Journal of Comparative Psychology*, 22: 128, August, 1936.

variable. In four cases, Nos. 4, 8, 9, and 28, only seven post-operative observations were made on account of a time shortage.

Histological methods. After the observations were completed the animals were killed and the brains removed and fixed in alcohol. They were then embedded in cellodin, sectioned fifty microns thick, and stained with thionin. In a few cases with small destructions in the critical region every section was saved, but in most instances only every fourth section was saved. Reconstructions of the lesions were made according to Lashley's technique[8] and the area of the destruction computed with a planimeter.

[8] Karl S. Lashley, Brain Mechanisms and Intelligence (Chicago: The University of Chicago Press, 1929), pp. 16-17.

periods. In four cases, [illegible] were given post-operative observations [illegible] shortage.

<u>Histological methods</u>. [illegible] completed the animals were killed [illegible] and fixed in alcohol. They were [illegible] in [illegible] and, sectioned [illegible] microns [illegible] thionin. In a few cases [illegible] critical region [illegible] for [illegible] stained only every [illegible] of the lesions were [illegible] [illegible] examination.

# CHAPTER II

## ANALYSIS AND INTERPRETATION OF THE DATA

General precautions. Before analysis and interpretation of results are possible it is necessary to observe several factors which must be controlled to give reliability to the experiment.

(a) First, it must be recognized that the results depend on the consistency of the records obtained in the observational periods. There can be no doubt of the reliability of a transfer in a single handed rat after a brain operation. But one cannot be so sure that a minor change in an ambidextrous rat, with somewhat variable records before the operation, is of great significance. Therefore, the results, in terms of percentages before and after the operation (Table III), have not been stressed. Instead, the animals have been classified according to effect of the operation into three groups: (1) transfer cases, those which used the hand contralateral to the site of the operation less than 2 per cent of the time; (2) affected cases, those whose hand contralateral to the site of the operation was used a smaller percentage of the time than before the operation; (3) unaffected cases, who showed no change or actually used the contralateral hand more often after the operation. It was recognized that these cases might include a group with homolateral effects.

(b) Individual variations in local areas have been

TABLE III

PERCENTAGE OF RIGHT-HANDEDNESS BEFORE AND AFTER THE OPERATION, LOCUS OF THE LESION AND PERCENTAGE OF DESTRUCTION

| Rat No. | Percent of Right-handedness before the operation | Percent of right-handedness after the operation | Locus of the lesion | Percent of Destruction |
|---|---|---|---|---|
| 3 F | 26 | 100 | R frontal | 2.8 to 8.8 |
| 4 F | 97 | 1 | L frontal | 6.8 |
| 5 F | 14 | 99 | R frontal | 6.4 to 10 |
| 6 F | 52 | 2 | L frontal | 1 |
| 7 F | 17 | 100 | R occiptal | 137.6 to 39.2 |
| 8 M | 83 | 1 | L occipital | 64.8 |
| 9 M | 11 | 79 | R occipital | 72.8 |
| 10 M | 86 | 21 | L occipital | 30 |
| 11 F | 69 | 31 | L occipital | 35.8 |
| 12 F | 29 | 85 | R frontal | 2.8 |
| 13 F | 50 | 26 | L frontal | 2 |
| 14 F | 83 | 42 | L frontal | 1.6 to 7.2 |
| 15 F | 46 | 91 | R pre-motor | 2 |
| 16 M | 10 | 68 | R pre-motor | 2.4 |
| 17 M | 40 | 64 | R pre-motor | 2.8 |
| 18 F | 95 | 68 | L pre-motor | 2 |
| 19 F | 2 | 11 | R pre-motor | 5.2 to 8.8 |
| 20 M | 84 | 96 | L frontal | 7.6 |
| 21 F | 98 | 99 | L frontal & occipital | 135.6 to 3.8 |
| 22 M | 96 | 100 | L frontal & occipital | 124.8 to 30.4 |
| 23 M | 97 | 99 | L occipital | 29.2 |
| 24 M | 99 | 100 | L occipital | 24.8 |
| 25 F | 3 | 1 | R occipital | 25.6 |
| 26 F | 95 | 100 | L occipital | 17.6 |
| 27 F | 95 | 97 | L occipital | 6 |
| 28 M | 74 | 89 | L occipital | 30.8 |
| 29 M | 18 | 3 | R occipital | 27.2 |

frequently reported in the literature. Peterson has mentioned variations within the electro-stimulable region in the rat.[9] Lashley has found considerable variation of the area striata from one animal to another, and has suggested that such variations are the result both of anatomical differences and of changed in physiological organization.[10] Any attempt to localize a function precisely by means of a common area of several transfer cases is defeated if such variations are too great. Such common areas reduce themselves to zero, and we would be forced to conclude that there was no localization of function. Yet, every transfer case may be within a few millimeters of some such locus, while the unaffected cases are considerably farther removed. Thus we are forced to admit a specialization of function within the cerebral cortex, withal the possibility of variation of any precise locus from one animal to another.

(c) Cortical lamination presents another type of specialization which must be considered in the analysis of the results. According to Craigie, the large pyramidal tract are found in layer V of the rat cortex.[11] If cortical transfers result only from injuries to this mechanism, then lesions invading more superficial layers of the cortex might have no influence on the handedness. Thus, the depth as well as the

---

[9] George M. Peterson, "Mechanisms of Handedness in the Rat," Comparative Psychology Monographs, No.6, 9: 23-24, April, 1934

[10] Karl S. Lashley, Brain Mechanisms and Intelligence (Chicago: The University of Chicago Press, 1929), p. 24.

[11] E. Horne Craigie, An Introduction to the Finer Anatomy of the Central Nervous System Based Upon That of the Albino Rat (Philadelphia: P. Blakeston's Sons and Company, 1925), p. 111.

extent of the destruction must be taken into consideration.

(d) It is difficult to interpret subcortical injuries because of our ignorance regarding the part played by various subcortical mechanisms on handedness. The subcortical mechanisms most frequently invaded in this study were the hippocampus, caudate nucleus, and thalamus. Hippocampal injuries are assumed to be ineffective in causing transfers, both for anatomical reasons, and because too many injuries of this type have failed to show effects. This cannot be said for the caudate nucleus and thalamus, and it is possible that transfers in some instances could be due to injuries to the subcortical structures rather than to a destroyed locus of the cerebral cortex. Less weight must be given to such cases in the interpretation of the results. An attempt to interpret results in the light of the size of the pyramidal tract in the cerebral peduncles gave negative results, since some cases, showing an obvious reduction in size failed to transfer in handedness, and other transfer cases failed to reveal a noticeable difference in size. This was to be expected since the tract carries fibers other than those specialized for hand and arm movements, but the attempt was made in an effort to control subcortical influences.

(e) Another factor which gives some difficulty in extent of the destruction [illegible]

(c) It is [illegible]

jected because of [illegible] by the [illegible]

by various substitutions [illegible]

Cortical [illegible]

were the hippocampus, [illegible]

Hippocampal [illegible]

causing tremors, [illegible]

too many [illegible]

This cannot [illegible]

and it is possible [illegible]

is due to injuries to [illegible]

them to [illegible]

weight was [illegible]

of the results [illegible]

light of the [illegible]

peduncles gave [illegible]

an obvious weakness [illegible]

ness, and other [illegible]

cable difference [illegible]

the most [illegible]

hand and arm [illegible]

effort to control [illegible]

(e) [illegible]

the precise localization of a critical area, is the inaccuracy of the brain charts used in plotting the lesions. The particular chart used is probably more in error in the frontal than the occipital regions, and it is in the frontal region that there is need of greatest accuracy. Lashley's new chart would be preferable, but it was not available soon enough for this study, and it is doubtful if any chart would be wholly satisfactory since individual differences in brain size would always produce some deviations.

An attempt was made to overcome this difficulty by an analysis in which the brain sections themselves were examined under overlapping conditions at comparable levels. The results thus obtained were used to supplement those results obtained from an analysis of the overlapping lesions outlined in the brain charts.

The percentage of right handedness before and after the operation, the locus and the extent of the destruction are given in Table III; the individual handedness records both before and after the operation are given in the Appendix.

Results. The results of the operation are divided into the following cases: transfer cases; affected cases; and unaffected cases.

Transfer cases. Eight cases transfered (Nos. 3, 4, 5, 6, 7, 8, 9, and 10). Four of these involved frontal destructions (Nos. 3, 4, 5, and 6), and four occipital

The predominant [illegible]
diameters of [illegible]
the parotid [illegible]
[illegible] region that [illegible]
[illegible]
soon enough [illegible]
[illegible]

An attempt [illegible]
an analysis [illegible]
obtained [illegible]
The results were [illegible]
[illegible]
function [illegible]

The percentage [illegible]
the operation, [illegible]
are given in Table [illegible]
both before and [illegible]

Location. [illegible]
into the following [illegible]
and unaffected [illegible]

Palatal [illegible]
[illegible] 12) [illegible]
deformities ([illegible]

destructions (Nos. 7, 8, 9, and 10). Of the frontal cases, No. 6 is especially noteworthy because of the small area of destruction, less than 1 per cent, which produced a transfer.

If a composite of the common area for all the transfer cases is drawn, the area completely vanishes because of rat No. 7, whose destroyed area had nothing in common with the rest of the transfer cases. A composite of the four frontal cases gives a common area which is shown in black in Figure I; the total area for all four cases in in outline. This common area is at level nine on the chart, and lies directly above the dorsal aspect of the caudate nucleus. It is 250 microns posterior to the genu of the corpus callosum. A comparison of the four occipital transfer cases with the common area of the frontal cases reveals that three of them (Nos. 8, 9, and 10) include all of it. The remaining case, No. 7, did not involve this common area, but a consideration of the subcortical invasion of this case reveals that the dorsal convexity of the caudate nucleus has been definitely invaded, especially in the region of level eleven. Even if the caudate nucleus itself were not a determining factor in handedness, its invasion would more than likely cut the pyramidal fibers coming from the region of level nine and involving the critical area for handedness. With the exception of this animal, the destructions

destructive (Nos. 2, 5, 8, and 10), or [illegible]
No. 8 is essentially unchanged in [illegible]
destruction, less [illegible]
fer.

If a comparison [illegible] thera-
fal cases is drawn, [illegible]
ity No. 7, whose destruction [illegible]
the rest of the [illegible]
frontal lobes [illegible]
in Figure 1, the [illegible]
lion. This common [illegible]
lies directly [illegible]
nucleus. It is [illegible]
pus callosum. [illegible]
cases with the common [illegible]
three of them (Nos. [illegible], and 11) [illegible]
remaining case, No. 7, [illegible]
a consideration of the [illegible]
reveals that the dorsal [illegible]
been definitely invaded, [illegible]
eleven. [illegible]
determining factor in [illegible], the [illegible]
than likely [illegible]
of level with [illegible]
ness. With the [illegible]

Fig. 1. A composite of four frontal transfer cases (Nos. 3, 4, 5 and 6) with the common area shown in black.

of all seven cases were deep enough to include layer V of the cortex and, at some parts of the lesion, included all six layers of the cortex.

One case, No. 11, with an occipital lesion which did not involve the common area, showed a temporary transfer with subsequent recovery. This temporary transfer may have been due to a blood clot or pressure on the cortex which gradually disappeared.

Transfers that occur from lesions in the occipital cortex could be due to an invasion of the local area, or to the destruction of pyramidal fibers descending from this area. It is difficult to explain them by the extent of the destruction. The smallest occipital lesion that caused a transfer was 30 per cent of one hemisphere in rat No. 10; case No. 21, which did not transfer, had a lesion which closely overlapped that of No. 10, amounting to 36 per cent of the hemisphere. Such facts do not conform with mass or gradient theories of cortical functioning.

Affected cases. There were eight affected cases (Nos. 12, 13, 14, 15, 16, 17, 18, and 19) in which the degree of transfer ranged from very marked to a very slight disturbance. In view of the minor fluctuations in ambidexterity, the latter cases could be regarded skeptically, but this is hardly true of the cases showing more marked changes. Since these cases are evidently not due to the

of all seven cases [illegible] the [illegible]
the cortex [illegible]
six layers of the cortex.

One case, No. 13, [illegible] did
not involve the [illegible]
with [illegible]
been due to a blood [illegible]
gradually [illegible].

Circulatory [illegible] in the [illegible]
cortex [illegible]
to the [illegible]
the [illegible]. It is [illegible]
of the [illegible]
[illegible]
(No. 10); case [illegible]
lesion which [illegible]
to be [illegible] of the [illegible]
form with [illegible]

Affected [illegible] [illegible]
(Nos. 12, 13, 14, 15, 16, [illegible])
degree of [illegible]
[illegible]. In [illegible]
[illegible]
but this is [illegible]
changes. [illegible]

unreliability of ambidexterity, it is assumed that these very slightly disturbed cases also indicate reliable changes as a result of the operation. Three animals in the affected group have lesions which partly invade the critical area (Nos. 12, 13, and 14). In one of these cases, No. 12, the contralateral hand was used about 15 per cent of the time after the operation. Its destruction, although somewhat larger, involved the same region of the cortex as rat No. 6, which used his affected hand only 2 per cent of the time. Both of these cases were very evenly divided in the use of their hands before the operation. The individual differences in these two cases are difficult to account for at the present time. The other two cases (Nos. 13 and 14) did not involve all of the critical area and their partial transfers could be accounted for by this fact; again, since they involve about the same amount of the critical area, the differences in their degree of transfer might be due to the fact that the one which showed the lesser effect was less ambidextrous before the operation.

Five cases with lesions considerable anterior to level nine were also affected (Nos. 15, 16, 17, 18, and 19). There are not enough cases here to offer an adequate study of the relative influence of the locus, distance from the critical area, size of the lesion, or the degree of ambidexterity before the operation, in determining the degree unreliability of handedness [illegible]

very slightly disturbed [illegible]

as a result of the operation. Three animals in the [illegible]

group have lesions which [illegible]

(Nos. [illegible], [illegible], and [illegible]). In each of these cases, [illegible]

contralateral [illegible]

after the operation. [illegible]

Larger, involved the same [illegible]

which used its affected [illegible]

Both of these cases [illegible]

their heads before the operation. [illegible]

in these two cases [illegible]

time. The other [illegible]

all of the [illegible]

be accounted for [illegible]

shows the same [illegible]

in their degree of [illegible]

the one which [illegible]

trous before the operation.

Five of [illegible]

level also were [illegible] (Nos. [illegible])

There are not [illegible]

of the relative [illegible]

critical area, [illegible]

dexterity before the operation, [illegible] of transfer which occurred. But there is an exception to the possibility that any one of these factors taken alone is the determining factor in producing the effect, if it were dependent on the degree of ambidexterity. Rat Nos. 15 and 17 should be more affected than Nos. 16 and 18, whereas they were influenced to a lesser degree by the operation. Similarily, if it were a function of mass, Nos. 17 or 19 with greater destructions should be more affected than No. 15 with the smallest destruction, but in reality No. 15 showed the greater effect. Again, if it were dependent upon its proximity to the critical region Nos. 15 and 16 should be less affected than Nos. 17 and 18, but they were actually more affected.

There are two other possibilities which may be considered. First, these cases might delimit a secondary handedness area, a sort of "premotor" cortex, in the vicinity of level five which acts as a facilitating mechanism upon the critical area. This seems unlikely since Lashley found that the entire frontal pole is electrically stimulable.[1] If a region that gives hand and arm movements when stimulated electrically turns out to be specialized for the control of these organs, should we not expect that another region which gives

[1] Karl S. Lashley, "The Motor Areas," Brain, 4: 255-258, 1921.

of trematar [illegible] [illegible]. [illegible] [illegible] to [illegible] account, to the possibility that some of the [illegible] [illegible] [illegible] if the degeneration [illegible] [illegible] [illegible] [illegible] were dependent on [illegible] [illegible] [illegible] 16 and 17 should [illegible] [illegible] [illegible] whereas they [illegible] [illegible] [illegible] [illegible] operation. [illegible] [illegible] [illegible] Nos. 17 [illegible] [illegible] [illegible] affected than [illegible] [illegible] [illegible] [illegible] in reality [illegible] [illegible] [illegible] [illegible] if were dependent upon [illegible] [illegible] [illegible] region Nos. 12 and 14 should [illegible] [illegible] [illegible] 12 and 15, but they [illegible] [illegible] [illegible].

There are two other [illegible] [illegible] [illegible] considered. First, [illegible] [illegible] [illegible] [illegible] [illegible] headhead area, [illegible] [illegible] [illegible] vicinity of [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] [illegible] since Lashley [illegible] [illegible] [illegible] electrically [illegible] [illegible] [illegible] and arm movements [illegible] [illegible] out to be [illegible] [illegible] [illegible] should we not [illegible] [illegible] [illegible]

---

[illegible] Karl S. Lashley, [illegible] [illegible] 257-258, 1921.

head or neck movements to be specialized for the control of these parts?

Secondly, frontal operations might interfer with the circulation of the blood through the anterior cerebral artery and thus disturb metabolism in the region of level 9. This appears less plausible when we remember that shallow lesions in the neighborhood of level 9 are ineffective if they do not invade layer V, yet they unquestionably disturb the superficial blood circulation.

Apparently, more critical data are necessary to interpret these r esults.

However, these cases as a group present strong evidence in favor of a "more or less" type of functioning rather than an "all or none" type suggested by Lashley in his recent study of the visual cortex.[2] This "more or less" functioning of a region was also noted in the case of gradual transfers and recoveries previously reported.[3] It is again possible to see a preferential use involving two mechanisms.

---

[2] Karl S. Lashley, "The Mechanism of Vision. XII. Nervous Structures Concerned in the Acquisition and Retention of Habits Based on Reactions to Light," Comparative Psychology Monographs, No. 2, 11: 74, February, 1935.

[3] George M. Peterson, "Mechanisms of Handedness in the Rat," Comparative Psychology Monographs, No. 6, 9: 39, April, 1934.

head or neck movements to [illegible] of these parts?

Secondly, [illegible] the circulation of the [illegible] cerebral artery and [illegible] of level [illegible] that double lesions [illegible] ineffective [illegible] unquestionably disturb the [illegible].

Apparently, [illegible] interpret these results.

However, these cases [illegible] evidence in favor of [illegible] rather than one [illegible] his recent study of [illegible] functioning of a region [illegible] gradual transfers and [illegible] is again possible to [illegible] mechanisms.

---

[1] Karl S. Lashley, [illegible] Nervous Structures Concerned in [illegible] of Habits Based on [illegible] Comparative Psychology Monographs, [illegible] 11: [illegible]

[2] George [illegible] Peterson, [illegible] April, 19[illegible]

<u>Non-affected cases</u>. Three cases with frontal operations (Nos. 20, 21, and 22), two of which also had occipital lesions (Nos. 21 and 22), and seven other cases with occipital lesions (Nos. 23, 24, 25, 26, 27, 28, and 29), were not affected by the operation. That is, these cases used their contralateral hands at least as often as before the operation. The lesions of the three frontal cases were very shallow, none of them invading deeper than the third layer of the cortex. In one of these cases, No. 20, the lesion unquestionably involved all of the critical area, and was sufficiently large ( 7.6 per cent) to have produced a transfer. The other two cases, Nos. 21 and 23, possessed large enough occipital lesions, 35.6 and 29.2 per cent, and enough of the critical area to have had an affect on their handedness on the basis of the results previously described. We may, therefore, assume that the cells which must be disturbed to produce transfers are below layer III and are probably the large pyramidal cells of layer V whose fibers form the pyramidal tract.

Two of the nine cases with occipital lesions, Nos. 21 and 23, involved parts of the critical area and were sufficiently deep to include layer V. It is somewhat surprising that they did not at least show an effect. However, since the critical area was only partially invaded, Non-striated cases. [illegible]

arians (Nos. 20, 21, and 26), [illegible]

pital lesions (Nos. [illegible]). [illegible]

with occipital lesions (Nos. 25, [illegible], and

80), were [illegible] by the [illegible]

cases used their [illegible]

before the operation. The [illegible] of the [illegible]

cases were very [illegible]

than the third [illegible]

No. 80, the [illegible]

cortical area, and [illegible])

to have produced [illegible]

21 and 26, [illegible]

25.0 and 25.6 per cent. [illegible]

to have had [illegible]

the [illegible]

assume that the [illegible]

[illegible]

[illegible] cells of [illegible]

[illegible] area.

Two of [illegible]

21 and 26, [illegible]

sufficiently [illegible]

[illegible]

area, since the [illegible]

we can assume either that enough of it remained intact to carry out the handedness function, or that there was sufficient displacement of the area in these two cases to make it less invaded than the microscopical analysis seemed to indicate; in other words, that these cases furnish two examples of individual variations.

The remaining occipital cases, Nos. 22, 24, 25, 26, 27, 28, and 29, were not influenced by the operation, or were influenced in the wrong direction, that is, they used their contralateral hands more often. Such a change could be regarded as a "homolateral" or inhibiting effect, in opposition to the contralateral or facilitating effect revealed by the frontal cases. This interpretation, however, can be regarded very skeptically for the following reasons. Seven of the occipital cases (Nos. 21, 22, 23, 24, 25, 26, and 27) were very slightly ambidextrous preferring one hand 95 per cent of the time, or more, before the operation, and revealing periods when they used one hand exclusively. Their change after the operation could be a continuation of this and thus lack significance from the stand point of an operational influence. Furthermore, a detailed examination of the two cases which were markedly affected (Nos. 28 and 29) reveals that they have somewhat variable records. Thus, although No. 28 used his left hand 26 per cent of the time on nine occasions before the

operation, he used it less than 10 per cent of the time on three of these occasions, which approximates his record after the operation. Similarly, No. 29 used his right hand only about 5 per cent of the time during the last six periods before the operation, although he used it an average of 18 per cent of the time throughout this period. His change to 3 per cent usage after the operation is not far out of line from this 5 per cent usage and hence less significant than if compared to his complete record. Finally, Rat No. 20 with a shallow frontal destruction may also have shown this homolateral or inhibitive effect, but again his change is in accord with his more recent record before the operation. Therefore, while all these cases may reveal such an effect, they are not decisive enough to be offered as conclusive evidence.

They are, however, strong evidence against any non-localization theory which assumes that all regions of the cerebral cortex function as a whole in the control of behavior. If the occipital cortex contributed a mass influence or a portion of a physiological gradient, the destructions would be expected to have a more or less effect on handedness, as happens with frontal injuries. The results obtained in these cases also make it obvious that the transfers occurring from the extensive destructions in cases 7, 8, 9, and 10 were due to the invasion of the

critical region or its underlying fiber tracts, and not to a destruction outside this frontal region.

# CHAPTER III

## SUMMARY AND CONCLUSIONS

Twenty-seven ambidextrous rats were subjected to a variety of cerebral operations mainly in the frontal and occipital cortex for the purpose of studying the relative influence of the locus and mass of destruction upon changes in handedness. Two additional rats were observed over a long time period to determine if ambidexterity is a sufficiently reliable index to be used as a criterion in a study of the cerebral control of this trait. The results indicate that although there are fluctuations and changes in the use of the hands by ambidextrous rats, the animals are sufficiently consistent to warrant the conclusion that persistent changes after cerebral extirpations are due to the operations and are not fortuitous, chance occurrances.

It was furthermore found that a small region in the contralateral frontal lobe is essential for the control of handedness by the cerebral cortex. This region is approximately 250 microns posterior to the genu of the corpus callosum, directly over the dorsal convexity of the caudate nucleus, and lies below layer III of the cortex, probably in layer V. Although its exact locus is somewhat variable from one animal to another, extirpations in

this region result in marked changes in the use of the hand. Injuries to other parts of the frontal lobe also influence the preferential use of the hands, but less markedly than destructions in this critical area. If such injuries are evidence for a facilitating function of the remainder of the frontal lobe, the conditions producing it are not revealed.

Injuries in the occipital and parts of the temporal region have no such effect upon the use of the hands. In fact, if these regions make any contribution to the control of this trait, it is an opposite effect to that expected; that is, the animals use their contralateral hands more often after such operations. That they contribute nothing to the control of the habit is clearly seen in the failure of these occipital injuries to produce a more or less effect as some of the frontal injuries did even when complete transfers did not result. The effects obtained from such occipital operations as were influential can be attributed to the invasion of the critical area or to the severance of fiber tracts which form the pyramidal system and descend from this area.

The results are compatible with localization theories of cerebral functioning but not with non-localization theories, such as mass action, equipotentiality, physiological gradients, etc.

From the results obtained, the following conclusions are drawn:

(1) Ambidexterity affords a sufficiently critical and reliable means of investigating the functioning of the cerebral cortex.

(2) The trait of handedness is under the control of a highly localized mechanism in the frontal region of the cerebral cortex, and large destructions outside the frontal lobe are ineffective in producing changes in this trait.

(3) The results support a localization theory and are in opposition to current non-localization theories.

# BIBLIOGRAPHY

BIBLIOGRAPHY


Craigie, E. Horne, An Introduction to the Finer Anatomy of the Central Nervous System Based Upon That of the Albino Rat. Philadelphia: P. Bladeston's Sons and Company, 1925. 127 pp.

Lashley, Karl S., "The Motor Areas," Brain, 44: 255-285, 1921.

_______, "Studies of Cerebral Function in Learning. VII. The Relation Between Cerebral Mass, Learning, and Retention," Journal of Comparative Neurology, 41: 1-58, 1926.

_______, Brain Mechanisms and Intelligence. Chicago: The University of Chicago Press, 1929. 186 pp.

_______, "Studies of Cerebral Function in Learning. VIII. A Reanalysis of Data on Mass Action in the Cerebral Cortex," Journal of Comparative Neurology, 54: 77-84, February, 1932.

_______, "The Mechanism of Vision. XII. Nervous Structures Concerned in the Acquisition and Retention of Habits Based on Reactions to Light," Comparative Psychology Monographs, No. 2, 11: 43-79, February, 1935.

Peterson, George M., "A Preliminary Report on Right and Left Handedness in the Rat," Journal of Comparative Psychology, 12: 243-250, August, 1931.

_______, "Mechanisms of Handedness in the Rat," Comparative Psychology Monographs, No. 6, 9: 1-67, April, 1934.

Peterson, George M. and Genevieve W. Carter, "The Local Application of Drugs to the Motor Cortex of the Rat," Journal of Comparative Psychology, 22: 123-129, August, 1936.

# APPENDIX

# APPENDIX

## TABLE IV

## RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 3 ♀ | | Rat No. 4 ♀ | | Rat No. 5 ♀ | | Rat No. 6 ♀ | | Rat No. 7 ♀ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 9 | 41 | 48 | 2 | 16 | 34 | 27 | 23 | 14 | 36 |
| 2 | 26 | 24 | 46 | 4 | 0 | 50 | 23 | 27 | 15 | 35 |
| 3 | 4 | 46 | 47 | 3 | 19 | 31 | 42 | 8 | 6 | 44 |
| 4 | 32 | 18 | 47 | 3 | 4 | 46 | 29 | 21 | 0 | 50 |
| 5 | 40 | 10 | 50 | 0 | 0 | 50 | 32 | 18 | 3 | 47 |
| 6 | 0 | 50 | 50 | 0 | 5 | 45 | 4 | 46 | | |
| 7 | 5 | 45 | 50 | 0 | 8 | 42 | 21 | 29 | | |
| 8 | 7 | 43 | 50 | 0 | 10 | 40 | 22 | 28 | | |
| 9 | 10 | 40 | | | 7 | 43 | 32 | 18 | | |
| 10 | 0 | 50 | | | 8 | 42 | 30 | 20 | | |
| 11 | 10 | 40 | | | 2 | 48 | 27 | 23 | | |
| 12 | 15 | 35 | | | 5 | 45 | 25 | 25 | | |

## APPENDIX

### TABLE IV (continued)

### POST-OPERATIVE RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 3 ♀ | | Rat No. 4 ♀ | | Rat No. 5 ♀ | | Rat No. 6 ♀ | | Rat No. 7 ♀ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 50 | 0 | 1 | 49 | 50 | 0 | 18 | 32 | 50 | 0 |
| 2 | 50 | 0 | 0 | 50 | 50 | 0 | 1 | 49 | 50 | 0 |
| 3 | 50 | 0 | 0 | 50 | 50 | 0 | 2 | 48 | 50 | 0 |
| 4 | 50 | 0 | 0 | 50 | 49 | 1 | 0 | 50 | 50 | 0 |
| 5 | 50 | 0 | 0 | 50 | 49 | 1 | 1 | 49 | 50 | 0 |
| 6 | 50 | 0 | 0 | 50 | 49 | 1 | 0 | 50 | 50 | 0 |
| 7 | 50 | 0 | 0 | 50 | 50 | 0 | 1 | 49 | 50 | 0 |
| 8 | 50 | 0 | | | 50 | 0 | 1 | 49 | 50 | 0 |
| 9 | 50 | 0 | | | 50 | 0 | 0 | 50 | 50 | 0 |
| 10 | | | | | | | 0 | 50 | 50 | 0 |
| 11 | | | | | | | 0 | 50 | 50 | 0 |
| 12 | | | | | | | 0 | 50 | 50 | 0 |
| 13 | | | | | | | 0 | 50 | 50 | 0 |
| 14 | | | | | | | 0 | 50 | 50 | 0 |
| 15 | | | | | | | 0 | 50 | 50 | 0 |
| 16 | | | | | | | 0 | 50 | 50 | 0 |
| 17 | | | | | | | 0 | 50 | 50 | 0 |
| 18 | | | | | | | 1 | 49 | | |
| 19 | | | | | | | 1 | 49 | | |
| 20 | | | | | | | 0 | 50 | | |
| 21 | | | | | | | 0 | 50 | | |
| 22 | | | | | | | 0 | 50 | | |
| 23 | | | | | | | 0 | 50 | | |
| 24 | | | | | | | 2 | 48 | | |

# APPENDIX

## TABLE IV (continued)

## RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 8 ♂ | | Rat No. 9 ♂ | | Rat No. 10 ♂ | | Rat No. 11 ♀ | | Rat No. 12 ♀ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 41 | 9 | 8 | 42 | 29 | 21 | 15 | 35 | 23 | 27 |
| 2 | 45 | 5 | 6 | 44 | 34 | 16 | 3 | 47 | 10 | 40 |
| 3 | 45 | 5 | 9 | 41 | 46 | 4 | 16 | 34 | 10 | 40 |
| 4 | 39 | 11 | 6 | 44 | 49 | 1 | 25 | 25 | 3 | 47 |
| 5 | 43 | 7 | 8 | 42 | 48 | 2 | 29 | 21 | 8 | 42 |
| 6 | 39 | 11 | 2 | 48 | 39 | 11 | 47 | 3 | 10 | 40 |
| 7 | 37 | 13 | 4 | 46 | 47 | 3 | 48 | 2 | 12 | 38 |
| 8 | 44 | 6 | 0 | 50 | 50 | 0 | 46 | 4 | 5 | 45 |
| 9 | | | | | | | 11 | 39 | 13 | 37 |
| 10 | | | | | | | 46 | 4 | 13 | 37 |
| 11 | | | | | | | 49 | 1 | 17 | 33 |
| 12 | | | | | | | 36 | 14 | 18 | 32 |
| 13 | | | | | | | 42 | 8 | 21 | 29 |
| 14 | | | | | | | 44 | 6 | 21 | 29 |
| 15 | | | | | | | 49 | 1 | 26 | 24 |
| 16 | | | | | | | 48 | 2 | 22 | 28 |
| 17 | | | | | | | 49 | 1 | | |
| 18 | | | | | | | 27 | 23 | | |

# APPENDIX

## TABLE IV (continued)

## POST-OPERATIVE RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 8 ♂ | | Rat No. 9 ♂ | | Rat No. 10 ♂ | | Rat No. 11 ♀ | | Rat No. 12 ♀ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 0 | 50 | 6 | 44 | 49 | 1 | 0 | 50 | 38 | 12 |
| 2 | 0 | 50 | 21 | 29 | 50 | 0 | 0 | 50 | 47 | 3 |
| 3 | 0 | 50 | 50 | 0 | 50 | 0 | 0 | 50 | 42 | 8 |
| 4 | 0 | 50 | 50 | 0 | 50 | 0 | 0 | 50 | 38 | 12 |
| 5 | 0 | 50 | 50 | 0 | 49 | 1 | 0 | 50 | 22 | 28 |
| 6 | 0 | 50 | 50 | 0 | 47 | 3 | 20 | 30 | 25 | 25 |
| 7 | 1 | 49 | 50 | 0 | 31 | 19 | 0 | 50 | 42 | 8 |
| 8 | | | | | 3 | 47 | 3 | 47 | 41 | 9 |
| 9 | | | | | 0 | 50 | 17 | 33 | 38 | 12 |
| 10 | | | | | 0 | 50 | 44 | 6 | 35 | 15 |
| 11 | | | | | 0 | 50 | 37 | 13 | 45 | 5 |
| 12 | | | | | 0 | 50 | 26 | 24 | 44 | 6 |
| 13 | | | | | 0 | 50 | 29 | 21 | 43 | 7 |
| 14 | | | | | 0 | 50 | 13 | 37 | 47 | 3 |
| 15 | | | | | 0 | 50 | 46 | 4 | 46 | 4 |
| 16 | | | | | 0 | 50 | 34 | 16 | 50 | 0 |
| 17 | | | | | 0 | 50 | 43 | 7 | 48 | 2 |
| 18 | | | | | 0 | 50 | 22 | 28 | 49 | 1 |
| 19 | | | | | 0 | 50 | 22 | 28 | 49 | 1 |
| 20 | | | | | 0 | 50 | 21 | 29 | 50 | 0 |
| 21 | | | | | 0 | 50 | 31 | 19 | 49 | 1 |
| 22 | | | | | 0 | 50 | 34 | 16 | 49 | 1 |
| 23 | | | | | | | 26 | 24 | | |
| 24 | | | | | | | 21 | 29 | | |
| 25 | | | | | | | 20 | 30 | | |
| 26 | | | | | | | 5 | 45 | | |
| 27 | | | | | | | 10 | 40 | | |

APPENDIX

TABLE IV (continued)

RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 13 ♀ | | Rat No. 14 ♀ | | Rat No. 15 ♀ | | Rat No. 16 ♂ | | Rat No. 17 ♂ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 13 | 37 | 33 | 17 | 38 | 12 | 1 | 49 | 27 | 23 |
| 2 | 32 | 18 | 45 | 5 | 32 | 18 | 2 | 48 | 23 | 27 |
| 3 | 28 | 22 | 42 | 8 | 30 | 20 | 0 | 50 | 26 | 24 |
| 4 | 37 | 13 | 43 | 7 | 32 | 18 | 2 | 48 | 17 | 33 |
| 5 | 11 | 39 | 42 | 8 | 23 | 27 | 8 | 42 | 26 | 24 |
| 6 | 21 | 29 | 42 | 8 | 19 | 31 | 1 | 49 | 12 | 38 |
| 7 | 29 | 21 | 43 | 7 | 14 | 36 | 10 | 40 | 16 | 34 |
| 8 | 26 | 24 | | | | | 17 | 33 | 14 | 36 |
| 9 | 23 | 27 | | | | | | | 19 | 31 |
| 10 | 28 | 22 | | | | | | | 21 | 29 |
| 11 | 32 | 18 | | | | | | | 21 | 29 |
| 12 | 28 | 22 | | | | | | | 14 | 36 |
| 13 | 16 | 34 | | | | | | | 18 | 32 |
| 14 | 26 | 24 | | | | | | | 20 | 30 |
| 15 | 27 | 23 | | | | | | | 17 | 33 |
| 16 | 24 | 26 | | | | | | | 12 | 38 |
| 17 | | | | | | | | | 19 | 31 |
| 18 | | | | | | | | | 17 | 33 |
| 19 | | | | | | | | | 25 | 25 |
| 20 | | | | | | | | | 19 | 31 |
| 21 | | | | | | | | | 21 | 29 |
| 22 | | | | | | | | | 23 | 27 |
| 23 | | | | | | | | | 29 | 21 |
| 24 | | | | | | | | | 27 | 23 |

APPENDIX

TABLE IV (continued)

POST-OPERATIVE RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 13 ♀ | | Rat No. 14 ♀ | | Rat No. 15 ♀ | | Rat No. 16 ♂ | | Rat No. 17 ♂ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 26 | 24 | 31 | 19 | 49 | 1 | 9 | 41 | 34 | 16 |
| 2 | 19 | 31 | 33 | 17 | 46 | 4 | 6 | 44 | 35 | 15 |
| 3 | 16 | 34 | 31 | 19 | 36 | 14 | 32 | 18 | 33 | 17 |
| 4 | 19 | 31 | 24 | 26 | 41 | 9 | 45 | 5 | 33 | 17 |
| 5 | 13 | 37 | 28 | 22 | 43 | 7 | 49 | 1 | 39 | 11 |
| 6 | 1 | 47 | 25 | 25 | 49 | 1 | 43 | 7 | 17 | 33 |
| 7 | 9 | 41 | 19 | 31 | 49 | 1 | 33 | 17 | 28 | 22 |
| 8 | 17 | 33 | 14 | 36 | 47 | 3 | 40 | 10 | 13 | 37 |
| 9 | 10 | 40 | 8 | 42 | 46 | 4 | 18 | 32 | 30 | 20 |
| 10 | 19 | 31 | 9 | 41 | 47 | 3 | 40 | 10 | 34 | 16 |
| 11 | 9 | 41 | 3 | 47 | 50 | 0 | 26 | 24 | 19 | 31 |
| 12 | 11 | 39 | 10 | 40 | | | 40 | 10 | 26 | 24 |
| 13 | 3 | 47 | 19 | 31 | | | 40 | 10 | 46 | 4 |
| 14 | 9 | 41 | 25 | 25 | | | 37 | 13 | 36 | 14 |
| 15 | 18 | 32 | 34 | 16 | | | 40 | 10 | 39 | 11 |
| 16 | 13 | 37 | 29 | 21 | | | 39 | 11 | 36 | 14 |
| 17 | 22 | 28 | 33 | 17 | | | 37 | 13 | 44 | 6 |
| 18 | 13 | 37 | 31 | 19 | | | 40 | 10 | | |
| 19 | 21 | 29 | 27 | 23 | | | | | | |
| 20 | 12 | 38 | 19 | 31 | | | | | | |
| 21 | 17 | 33 | 12 | 38 | | | | | | |
| 22 | 15 | 35 | 18 | 32 | | | | | | |
| 23 | 10 | 40 | 21 | 29 | | | | | | |
| 24 | | | 22 | 28 | | | | | | |
| 25 | | | 16 | 34 | | | | | | |
| 26 | | | 18 | 32 | | | | | | |
| 27 | | | 13 | 37 | | | | | | |

APPENDIX

TABLE IV (continued)

RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 18 ♀ | | Rat No. 19 ♀ | | Rat No. 20 ♂ | | Rat No. 21 ♀ | | Rat No. 22 ♂ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 50 | 0 | 4 | 46 | 31 | 19 | 50 | 0 | 44 | 6 |
| 2 | 48 | 2 | 0 | 50 | 14 | 36 | 47 | 3 | 49 | 1 |
| 3 | 47 | 3 | 1 | 49 | 40 | 10 | 48 | 2 | 50 | 0 |
| 4 | 49 | 1 | 0 | 50 | 48 | 2 | 50 | 0 | 49 | 1 |
| 5 | 48 | 2 | 1 | 49 | 44 | 6 | 50 | 0 | 50 | 0 |
| 6 | 42 | 8 | 0 | 50 | 36 | 14 | 48 | 2 | 50 | 0 |
| 7 | 48 | 2 | 1 | 49 | 40 | 10 | 49 | 1 | 50 | 0 |
| 8 | 50 | 0 | | | 43 | 7 | 50 | 0 | 46 | 4 |
| 9 | 47 | 3 | | | 42 | 8 | | | 47 | 3 |
| 10 | | | | | 43 | 7 | | | 50 | 0 |
| 11 | | | | | 48 | 2 | | | 50 | 0 |
| 12 | | | | | 49 | 1 | | | 50 | 0 |
| 13 | | | | | 46 | 4 | | | 49 | 1 |
| 14 | | | | | 49 | 1 | | | 50 | 0 |
| 15 | | | | | 50 | 0 | | | 50 | 0 |
| 16 | | | | | 45 | 5 | | | | |

APPENDIX

TABLE IV (continued)

POST-OPERATIVE RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 18 ♀ | | Rat No. 19 ♀ | | Rat No. 20 ♂ | | Rat No. 21 ♀ | | Rat No. 22 ♂ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 43 | 7 | 16 | 34 | 44 | 6 | 50 | 0 | 50 | 0 |
| 2 | 2 | 48 | 5 | 45 | 50 | 0 | 50 | 0 | 50 | 0 |
| 3 | 13 | 37 | 9 | 41 | 47 | 3 | 49 | 1 | 50 | 0 |
| 4 | 34 | 16 | 8 | 42 | 49 | 1 | 49 | 1 | 50 | 0 |
| 5 | 32 | 18 | 7 | 43 | 48 | 2 | 48 | 2 | 50 | 0 |
| 6 | 45 | 5 | 8 | 42 | 48 | 2 | 49 | 1 | 50 | 0 |
| 7 | 36 | 14 | 6 | 44 | 47 | 3 | 50 | 0 | 50 | 0 |
| 8 | 33 | 17 | 13 | 37 | 50 | 0 | 50 | 0 | 50 | 0 |
| 9 | 35 | 15 | 10 | 40 | 48 | 2 | 50 | 0 | 50 | 0 |
| 10 | 34 | 16 | 12 | 38 | 49 | 1 | 50 | 0 | | |
| 11 | 40 | 10 | | | 50 | 0 | | | | |
| 12 | 35 | 15 | | | | | | | | |
| 13 | 42 | 8 | | | | | | | | |
| 14 | 40 | 10 | | | | | | | | |
| 15 | 34 | 16 | | | | | | | | |
| 16 | 37 | 13 | | | | | | | | |
| 17 | 22 | 28 | | | | | | | | |
| 18 | 39 | 11 | | | | | | | | |
| 19 | 40 | 10 | | | | | | | | |
| 20 | 39 | 11 | | | | | | | | |
| 21 | 37 | 13 | | | | | | | | |

# APPENDIX

## TABLE IV (continued)

## RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 23 ♂ Right | Rat No. 23 ♂ Left | Rat No. 24 ♂ Right | Rat No. 24 ♂ Left | Rat No. 25 ♀ Right | Rat No. 25 ♀ Left | Rat No. 26 ♀ Right | Rat No. 26 ♀ Left | Rat No. 27 ♀ Right | Rat No. 27 ♀ Left |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 50 | 0 | 40 | 10 | 0 | 50 | 48 | 2 | 45 | 5 |
| 2 | 50 | 0 | 19 | 31 | 0 | 50 | 45 | 5 | 47 | 3 |
| 3 | 50 | 0 | 7 | 43 | 1 | 49 | 46 | 4 | 50 | 0 |
| 4 | 50 | 0 | 41 | 9 | 0 | 50 | 48 | 2 | 46 | 4 |
| 5 | 50 | 0 | 44 | 6 | 0 | 50 | 50 | 0 | 43 | 7 |
| 6 | 49 | 1 | 46 | 4 | 0 | 50 | 50 | 0 | 50 | 0 |
| 7 | 50 | 0 | 45 | 5 | 0 | 50 | 50 | 0 | 46 | 4 |
| 8 | 48 | 2 | 49 | 1 | 0 | 50 | 48 | 2 | 48 | 2 |
| 9 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 47 | 3 |
| 10 | 50 | 0 | 50 | 0 | 0 | 50 | 49 | 1 | 46 | 4 |
| 11 | 37 | 13 | 50 | 0 | 0 | 50 | 50 | 0 | 48 | 2 |
| 12 | 39 | 11 | 50 | 0 | 1 | 49 | 49 | 1 | 48 | 2 |
| 13 | 47 | 3 | 50 | 0 | 0 | 50 | 50 | 0 | 49 | 1 |
| 14 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 49 | 1 |
| 15 | 50 | 0 | 50 | 0 | 0 | 50 | 48 | 2 | 49 | 1 |
| 16 | 50 | 0 | 50 | 0 | 0 | 50 | | | | |
| 17 | 50 | 0 | 50 | 0 | 0 | 50 | | | | |
| 18 | 50 | 0 | 50 | 0 | 1 | 49 | | | | |
| 19 | 50 | 0 | 50 | 0 | 0 | 50 | | | | |
| 20 | 50 | 0 | 48 | 2 | | | | | | |
| 21 | 50 | 0 | 49 | 1 | | | | | | |
| 22 | 50 | 0 | 49 | 1 | | | | | | |
| 23 | 49 | 1 | 50 | 0 | | | | | | |
| 24 | 50 | 0 | | | | | | | | |
| 25 | 50 | 0 | | | | | | | | |

## APPENDIX

### TABLE IV (continued)

### POST-OPERATIVE RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 23 ♂ | | Rat No. 24 ♂ | | Rat No. 25 ♀ | | Rat No. 26 ♀ | | Rat No. 27 ♀ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Right | Left | Right | Left | Right | Left | Right | Left | Right | Left |
| 1 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 48 | 2 |
| 2 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 48 | 2 |
| 3 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 45 | 5 |
| 4 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 47 | 3 |
| 5 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 48 | 2 |
| 6 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 48 | 2 |
| 7 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 49 | 1 |
| 8 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 50 | 0 |
| 9 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 50 | 0 |
| 10 | 50 | 0 | 50 | 0 | 0 | 50 | 50 | 0 | 50 | 0 |
| 11 | 49 | 1 | 50 | 0 | 1 | 49 | 50 | 0 | 49 | 1 |
| 12 | | | | | 0 | 50 | | | | |

APPENDIX

TABLE IV (continued)

RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 28 ♂ | | Rat No. 29 ♂ | |
|---|---|---|---|---|
| | Right | Left | Right | Left |
| 1 | 49 | 1 | 31 | 19 |
| 2 | 48 | 2 | 2 | 48 |
| 3 | 46 | 4 | 7 | 43 |
| 4 | 42 | 8 | 20 | 30 |
| 5 | 29 | 21 | 17 | 33 |
| 6 | 8 | 42 | 21 | 29 |
| 7 | 43 | 7 | 29 | 21 |
| 8 | 41 | 9 | 11 | 39 |
| 9 | 39 | 11 | 12 | 38 |
| 10 | | | 2 | 48 |
| 11 | | | 1 | 49 |
| 12 | | | 2 | 48 |
| 13 | | | 5 | 45 |
| 14 | | | 3 | 47 |
| 15 | | | 20 | 30 |
| 16 | | | 2 | 48 |
| 17 | | | 6 | 44 |
| 18 | | | 13 | 37 |
| 19 | | | 5 | 45 |
| 20 | | | 7 | 43 |
| 21 | | | 0 | 50 |
| 22 | | | 3 | 47 |
| 23 | | | 1 | 49 |
| 24 | | | 0 | 50 |

# APPENDIX

## TABLE IV (continued)

## POST-OPERATIVE RECORDS IN THE FOOD SITUATION

| Observation period | Rat No. 28 ♂ | | Rat No. 29 ♂ | |
|---|---|---|---|---|
| | Right | Left | Right | Left |
| 1 | 45 | 5 | 1 | 49 |
| 2 | 35 | 15 | 3 | 47 |
| 3 | 48 | 2 | 1 | 49 |
| 4 | 50 | 0 | 0 | 50 |
| 5 | 50 | 0 | 2 | 48 |
| 6 | 46 | 4 | 3 | 47 |
| 7 | 44 | 6 | 1 | 49 |
| 8 | 50 | 0 | 2 | 48 |
| 9 | 50 | 0 | 1 | 49 |
| 10 | 50 | 0 | 0 | 50 |
| 11 | 50 | 0 | 0 | 50 |
| 12 | 50 | 0 | | |
| 13 | 5 | 0 | | |
| 14 | 6 | 4 | | |
| 15 | 7 | 6 | | |