

THE MAIN AFFERENT FIBER SYSTEMS
OF THE CEREBRAL CORTEX
IN PRIMATES

An Investigation of the Central Portions of the
Somato-sensory, Auditory, and Visual Paths of
the Cerebral Cortex, with Consideration of their
Normal and Pathological Function, based on
Experiments with Monkeys

BY

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4. IV. On <i>Leidyopsis sphaerica</i> gen. nov., sp. nov. Pp. 99-116, plates 13-14, 1 figure in text25
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6. A Critical Review of the Nomenclature of Human Intestinal Flagellates, <i>Cercomonas</i>, <i>Chilomastix</i>, <i>Trichomonas</i>, <i>Tetratrichomonas</i>, and <i>Giardia</i>, by C. A. Kofoid. Pp. 145-168, 9 figures in text35
7. On the Free, Encysted, and Budding Stages of <i>Councilmania taftewi</i>, a Parasitic Amoeba of the Human Intestine, by C. A. Kofoid and Olive Swezy. Pp. 169-198, plates 18-22, 3 figures in text60
8. Mitosis and Fission in the Active and Encysted Phases of <i>Giardia enterica</i> (Grassi) of Man, with a Discussion of the Method of Origin of Bilateral Symmetry in the Polymastigote Flagellates, by C. A. Kofoid and Olive Swezy. Pp. 199-234, plates 23-26, 11 figures in text50
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VOLUME 2

HERBERT McLEAN EVANS
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EDITORS

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FOREWORD

The investigations of the three chief afferent fiber systems in primates published herein represent only part of a more extensive experimental study of the fiber systems of the cerebral cortex. The original object of this study was to investigate the comparatively little known association connections of various cortical areas as determined by cytoarchitectural and myeloarchitectural investigations. The necessity for such a systematic investigation of association and other fiber systems according to cortical areas and regions was plainly recognized by C. and O. Vogt (1919, pp. 286, 287; 1929) and by Economo-Koskinas. In the course of this work, however, it soon became evident that knowledge of the association connections alone would be of little value unless the afferent paths and their terminal areas or regions in the cortex were well-known. For this reason attention was directed to the study of the three main afferent paths: the somatic sensory, the auditory, and the visual. The selection of these afferent paths can easily be understood in the light of their preponderant importance in the mental processes and others related thereto, in man and other primates.

In general the importance of knowledge of the afferent paths for understanding the cerebral mechanism and its function has been fully recognized by a series of investigators. In Henschen's (1918, p. 438) opinion,

A knowledge of the position, of the extent, and of the organization of the primary sensory regions (that is, of the projection fields of the cerebral cortex) is the foundation of anatomical-physiological brain-psychology, and is therefore the indispensable requirement and the first problem to be solved before we can form a clear anatomical idea of the processes involved in the creation of the mind.

The ultimate goal of this as of any other brain research is well formulated by Flechsig (1927, p. 120):

The main problem for the future undoubtedly will be an all-embracing psycho-physiology; otherwise in the future, as has happened in the past, positive knowledge will be menaced by an overgrowth of the mystic element;

and again by Henschen (1919, p. 58):

Since the mind depends on the function of our sense organs, it is evident that a knowledge of the localization, the extent, and the delimitation as well as of the anatomical organization, and physiological performances of our cerebral sensory areas represents the foundation of a scientific psychology, and that progress in our understanding of psychic processes depends on full clarity concerning the gateways of the afferent impulses from the source of experience.

A good exposition of this whole problem was given by C. and O. Vogt (1919, pp. 281 ff.). These ideas of Flechsig, of Henschen, and of the Vogts mean, of course, neither more nor less than that the ultimate aim of brain research should be the explanation of psychic processes and their related phenomena in terms of natural science, by means of anatomy, physiology, chemistry, physics, and so forth.¹ While it might seem inadvisable to aim directly at a goal which at present appears so distant, without doubt the only way toward it is that common to every branch of natural science, involving in this case the assistance afforded by knowledge of the anatomy, the histology, and the physiology of the brain, and above all of the cerebral cortex. In spite of the difficulties, the only justifiable course seems to be to resume the attack upon the problem with more and more perfect methods of investigation.

In addition to the desirability of a rational, scientific explanation of the highest nervous processes, there are other reasons of a more immediate, practical nature why a thorough knowledge of the cerebral fiber systems is desirable. One of these is the need for an understanding of certain physiological processes, such as the various forms of somatic sensations, audition, and vision. Furthermore, knowledge of the main fiber systems cannot fail to be of value to human pathology. During this work, therefore, there has been a special effort made to draw from the anatomical results valid conclusions concerning the pathogenesis, symptomatology, and diagnosis of lesions involving the three afferent paths investigated; the reader will judge how far this has been realized.

The extensiveness of the subject precludes detailed discussion even of the more important works of previous investigators. But all the publications listed in the terminal bibliography have received careful consideration, together with many others not cited. (For further references one may consult Alexander-Marburg, Ariens Kappers 1920-21, Bechterew, Bergmark, Brodmann 1909/1925, Brouwer-Zeeman 1926, Brown 1927, Ramón y Cajal, Economo-Koskinas, Foerster 1927, Goldstein 1927, Head, Herrick 1926, Klüver, Lashley 1929, Minkowski 1923-24, Monakow 1914, Overbosh, R. A. Pfeifer, Piéron, Schwab, Stopford, and Vogt.)

The investigations reported in this book were undertaken five years ago with the help of the Behavior Research Fund in Chicago, and were made possible by the grant of a fellowship from the Rocke-

¹ See also Herrick, 1929, 172 ff.

feller Foundation. It was primarily through the interest and the kind mediatorship of Professor C. J. Herrick of the University of Chicago that these experiments were undertaken and the valuable cooperation of Dr. K. S. Lashley was secured. Part of the examination of the material was carried out at the University of Chicago (Department of Anatomy), part at the Neurological Clinic of the University of Zagreb, Yugoslavia, part at the University of California (Department of Anatomy), Berkeley, and a part at the University of Chicago (Department of Medicine), all of which contributed their share of material help. The work was also supported by a grant from the Otho S. A. Sprague Memorial Institute, and by a grant from the Douglas Smith Foundation for Medical Research of the University of Chicago. Friends have helped in the revision of the English text and for this I wish to express my thanks to Mr. Lamar Jackson, Turlock, California, to Mrs. Miriam Goldeen, Berkeley, to Miss C. M. Flinn, Berkeley, to Mr. B. Brownfield, and especially to Professor I. Maclaren Thompson of the University of California, Berkeley, as also to Professor R. R. Grinker (Chicago) and to my wife Donna. Thanks have to be expressed to Dr. L. Wiley for his kind assistance in the experiments. Acknowledgment is due also to the University of California for the publication of the work with its numerous costly illustrations; and to Miss Gladys Alvarez for the trying task of typing the manuscript. Gratitude is expressed for the help in making numerous series of sections to Miss R. Bigelow (Chicago), and to Miss J. Newson (Chicago) for the help in preparing the manuscript. It is a pleasure to acknowledge the kind interest and support of Professor M. N. Lapinsky (Belgrade), of Professor K. S. Lashley (Chicago), of Professor G. W. Bartelmez (Chicago), of Professor P. Bailey (Chicago), and of Professor F. C. McLean (Chicago), whereby the work has been furthered. For being able to prosecute this work successfully and to finish it I feel obliged especially to thank Professor H. M. Evans, head of the Department of Anatomy at the University of California, for his great interest in this work, for his liberal support, for his unusual kindness in correcting the entire manuscript, and for the arrangement of the publication.

*. . . . une anatomie sans
physiologie serait une
anatomie sans but.*

—Flourens 1842, Preface p. 23

CONTENTS

	PAGE
FOREWORD.....	vii
CHAPTER I. Introduction.....	1
CHAPTER II. Problems.....	4
CHAPTER III. Material and Methods.....	17
PART I. SOMATIC SENSORY SYSTEM	
CHAPTER IV. Thalamic Termination of Afferent Somato-sensory Fiber Tracts. Intrathalamic Fiber Systems.....	23
CHAPTER V. Origin, Course, and Termination of Somato-sensory Thalamo-cortical and Thalamo-striate Fibers.....	27
CHAPTER VI. Extent and Boundaries of the Somato-sensory Cortex.....	47
CHAPTER VII. Cortical Terminations of Somato-sensory Afferent Fibers.....	55
CHAPTER VIII. Function and Disturbances of the Somato-sensory Radiation and of the Somato-sensory Projection Cortex.....	65
CHAPTER IX. Results of the Present Investigations of the Somatic Sensory System.....	70
1. Afferent somato-sensory tracts from lower regions of the neuraxis to the thalamus.....	70
2. Descending cortico-thalamic and other cortico-fugal fibers.....	71
3. Somato-sensory radiation.....	72
4. Boundaries of the somato-sensory projection cortex.....	74
5. Cortical terminations of the somato-sensory afferent fibers.....	76
6. Function of the somato-sensory projection cortex.....	77
PART II. AUDITORY SYSTEM	
CHAPTER X. Origin, Course, Termination, and Internal Organization of the Auditory Radiation.....	81
CHAPTER XI. Location, Extent, and Function of the Auditory Cortex.	87
1. Boundaries of the auditory projection cortex. Cortical terminations of the auditory fibers.....	87
2. Probable functional significance of the posterior Sylvian receptive region.....	90
CHAPTER XII. An Attempt to Explain the Minute Function of the Auditory System.....	92
CHAPTER XIII. Results of the Present Investigations of the Auditory System	101
1. Auditory radiation.....	101
2. Boundaries of the auditory projection cortex. Internal organization, function, and disturbances of the auditory radiation and of the auditory projection cortex.....	102

PART III. VISUAL SYSTEM

	PAGE
CHAPTER XIV. Origin, Course, and Termination of the Visual Radiation. Location and Extent of the Visual Projection Cortex. Projection of the Lateral Geniculate Body upon the Striate Area. (Findings).....	107
CHAPTER XV. Cortical Terminations of Visual Afferent Fibers (Findings)....	153
CHAPTER XVI. Visual System (Discussion).....	157
1. Visual radiation; its subcortical origin, its course, and its cortical termination.....	162
2. Internal organization of the visual radiation. Projection of the retina upon the visual radiation.....	167
3. Projection of the retina upon the cerebral cortex.....	172
4. Function and disturbances of the visual radiation and of the visual projection cortex.....	183
5. Organization and function of the visual system in general.....	189
6. Remarks on the comparative anatomy of the visual projection cortex	197
CHAPTER XVII. Results of the Present Investigations of the Visual System ...	199
1. Visual radiation. Boundaries of the visual projection cortex. Cor- tical terminations of the visual afferent fibers.....	199
2. Internal organization of the visual radiation.....	201
3. Projection of the retina upon the visual radiation and upon the cerebral cortex. Function and disturbances of the visual radiation and of the visual projection cortex.....	202
4. Organization and function of the visual system in general.....	205

PART IV. GENERAL CONSIDERATIONS

CHAPTER XVIII. General Considerations of the Relationship of the Afferent Paths to the Cerebral Cortex.....	211
CHAPTER XIX. An Attempt to Explain Structural Features of the Afferent Paths in Connection with their Function and their Bio- logical Significance.....	219
CHAPTER XX. Remarks on Future Investigation of the Cerebral Cortex.....	227

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CHAPTER I INTRODUCTION

Without minimizing our knowledge of the organization and function of the cerebral cortex, the need of a thorough, systematic study of the connections of the various cytoarchitectural areas and regions is clear. The cytoarchitectural and myeloarchitectural delimitation of cortical areas and the physiological and pathological investigation of special, circumscribed portions of the cortex, important and indispensable though they be, do not give a fully satisfactory answer concerning the functions of these areas and regions. For that answer the areal and regional connections must be known. To understand the distinctive function of the cortex the same fundamental problem encountered in other parts of the nervous system must be solved, namely, that of connections or interrelationships. While other branches of the investigation of the brain—physiology, psychology, and pathology—deal preponderantly or even exclusively with the elusive dynamic changes of the nervous substance and their frequently ambiguous manifestations, anatomy has to disclose special structures, neuronie complexes, fiber systems, and agglomerations of nerve cells which serve as the material substratum of these activities. Study of the fiber connections of the forebrain cortex will demonstrate the paths of spread of nervous impulses from the peripheral receptor organs to the cortex, the paths in the cortex itself, and back again from the cortex to the subcortical mechanisms and to various executive organs of the body; thus it will necessarily influence our conception of the organization and function of the brain.

Our current conception of the structure and function of the cortex is somewhat as follows: The cerebral cortex is a composite organ consisting of numberless nerve cells and fibers arranged for the most part in regular, parallel layers. Though almost everywhere essentially the same, these cell layers, as well as those of the intracortical fibers, exhibit, according to locality, considerable variation in the

number, size, shape, and arrangement of their structural elements. By these criteria a great number of cortical areas have been delimited, some with quite sharp boundaries, others apparently presenting a gradual transition to the neighboring areas. The number of these areas has not as yet been determined definitely, and it is found to increase as new methods of investigation are devised. The local variations in cortical structure force upon us the idea of diversified function, since everywhere else in the organism specialization in function goes hand in hand with structural change; hence the conception of diversified local functioning of the cortex has gained favor in the past few decades. Such a conception stands, on the whole, in good accord with numerous physiological experiments and clinical observations; it is at present recognized by the majority of neurologists as a general principle of the organization and function of the cortex ("Principle of Localization"; compare Campbell 1905, G. Elliot Smith 1907, 1909, Brodmann 1909, Vogt 1919, Economo-Koskinas 1925). Thus the cortex appears as a composite organ comprising a great number of special organs and suborgans (in the human hemisphere, according to Vogt, about 200), some of them, at least, having a function of their own (compare Brodmann 1909, Flechsig 1920, p. 44, and 1927, Herrick 1927; see especially the experiments of Vogt 1919, pp. 399 ff.). The complexity of mental processes, however, and of their correlated expressive acts in higher mammals, especially in man, suggests that the more complex psychic phenomena may be compound results of the activities of several cortical areas working together and probably assisted by subcortical nuclear masses. If one recognizes in general the close relationship between cortical structures and certain psychic manifestations—and much evidence from human and comparative anatomy, physiology, and pathology forces one toward such a conception—then it is evident that any attempt to explain subjective psychic phenomena in terms of natural science, in objective formulae of anatomy and physiology, must first define the relationship between certain psychic experiences and their objective manifestations on the one hand, and certain cortical localities or structures on the other. The first task of research is manifestly that of analysis, before a synthetic reconstruction of the mental mechanisms and their possible workings can be attempted.

How far has modern investigation succeeded in elucidating the fundamental organization of the brain and in explaining its essential function? It must be admitted that, though great progress was made

during the past decades, the mechanisms of mental processes, the cortical organs involved in these, and the means and modes of their integration remain for the most part imperfectly understood. As will be shown in the course of this treatise, a close acquaintance with the subject soon makes it evident that not only in many minor problems is there uncertainty, but that some major conceptions regarded at present as fairly well established can scarcely survive an impartial critical examination, while others need the corroboration of new investigations. No wonder that the old problem of the localization of cerebral functions is again raised. Though the doctrine that the circumscribed areas of the cortex have a distinctive function is accepted by the majority of neurologists in some form or other, we observe a tendency in modern times again to question the strictly localistic viewpoint. The alternative conception, especially noticeable in certain currents of modern experimental psychology and in many physiological and clinical works (compare Head, Berze, Goldstein, Monakow-Mourgue, Köhler, Schröder, Hines, Collier, Brugia, Niessl von Mayendorf, *et al.*), may be termed "equipotentialistic" and approaches more or less the ancient doctrine of Carus, Longet, Vulpius, Flourens, Goltz, and others of the functional omnivalence, or equivalence, of the entire cerebral cortex. Though there may perhaps be certain localities of the cerebral cortex connected with simple receptive processes, modern omnipotentialists assert that all major activities of the brain, and perhaps even the functions which appear as "partial," are products of the working of many areas and regions of the cortex or even of the entire brain. (Compare Chapter XVIII and the footnote to p. 217.)

In searching for the cause of these differences of opinion, one perceives that it lies mainly in the *relative* value placed upon the arguments on which the modern localistic doctrine is built up. Many of these arguments are not sufficiently convincing to eliminate the influence of personal opinion. This in turn is due largely to the absence of reliable anatomical data, as justly pointed out by Vogt (1919, pp. 285, 444), and as will be shown later in this treatise. This leads some to deny any intimate relationship between definite functions and cortical localities and to explain all higher cerebral processes by "dynamic" factors; it, also, accounts for the comparatively scant attention bestowed by psychologists and psychiatrists upon cerebral anatomy and physiology, though it must be admitted that this is partly due to the failure of modern brain anatomy to cooperate with these sciences in intensive attacks upon major problems.

CHAPTER II

PROBLEMS

The cerebral cortex may be regarded as a resonance chamber of external happenings, as a transformer and place of synthesis of exogenous impulses, and as an executor of its own decisions (these being evoked by external stimuli or by their internal residua); *any attempt to disclose the nature of cortical processes—that is, the fate of the incoming impulses from the external world—must commence by tracing the afferent paths traversed by these external impulses on their way to the cortex.* To explain adequately what happens to various external impulses in the cortex itself or how they are utilized and combined one with another by the cortical structures before being manifested as various effector actions, we must definitely settle other preliminary problems. For obviously the fate of the impulses reaching the cortex depends primarily on the organization of the afferent paths and on the mode of their relation to the cerebral cortex (compare Hensehen 1918, p. 438, and 1919, p. 58).

The first task is that of disclosing the anatomical identity of functionally distinct afferent paths from their peripheral receptor organs to their cortical terminations. Are there within the cerebral hemispheres anatomically definable fiber systems, distinct for each of the main afferent impulses (somato-sensory, auditory, visual, and so forth) and terminating in definite, well circumscribed, and relatively small cortical areas, delimited by sharp lines or boundaries, or, on the contrary, do some or all of these impulses use diffusely arranged (or perhaps multiple and differently organized) paths terminating in extensive and ill-defined cortical regions, and thus enter the cortex by several rather widely separated “gateways”?

The second and no less important problem is that of the internal organization of the afferent paths. There are substantial reasons for assuming that the forms or qualities of various impulses reaching the cortex, in addition to other factors, depend largely on the mutual relationship of the neurons composing these afferent paths.

Only after these problems find a satisfactory solution can an attack be made on the following question: By what paths and mechanisms are the impulses streaming into the cortex distributed and combined to form higher, complex forms of cortical activity? This latter prob-

lem demands above all anatomical investigation of the association, callosal, efferent, and other fiber systems of each of the known cyto-architectural areas or at least regions. Not before this has been settled and the main paths for diffusion of the nervous impulses disclosed, can *the finer problems of the cortex* be studied successfully; this is particularly true of the question of *the functional significance of the minute cortical structures and elements* as revealed by Golgi's and similar methods.

Thus, only by following the course of special impulses from the peripheral receptors along their special paths to their special cortical "gateways" and from these latter to other cortical areas and regions, in connection with physiological and pathological investigations, can an adequate conception of the fundamental processes of the cerebral cortex be achieved.

Scarcely more than the main facts concerning the central portions of the afferent paths, their cortical terminations, and their internal organization is now possessed by us. It is true that the majority of modern neurologists maintain that the main questions of the organization and working of the brain are, on the whole, satisfactorily solved. For example, we know, approximately at least, the position of the somatic sensory, the auditory, and the visual paths and their respective cortical terminal regions. There is likewise fair agreement as to the boundaries of the cortical "primary" or projection areas. What still remains to be settled consists, in their opinion, merely of minor problems or of the details of finer organization.

But a contrary opinion claims consideration. In the formulation of some modern views the interpretation of the data has certainly not always been sufficiently objective. It could be shown that important facts which did not confirm certain favored conceptions either have not received adequate consideration or have been entirely disregarded. For this reason, some ideas must still be regarded as insufficiently founded, needing further study; and others, as the present study will show, must be abandoned and replaced.

A few examples may be given. I mention first the *extent of the somatic sensory cortex and its relationship to the motor cortex*. (Compare also Bechterew, Monakow, 1914, p. 271; Bergmark, Economo-Koskinas, pp. 503, 532, 538.) As is well known, the dispute between the unitarian and the dualistic conception regarding the relation of the cortical "sensorium" and "motorium" which arose immediately after the discovery by Fritsch and Hitzig of the electrically

excitable region of the hemisphere, has in the course of time been settled against the unitarian view (Munk, Exner, Luciani, Bastian, Déjérine, Rothmann, Horsley, Head) in favor of the view of complete separation of the motor and somato-sensory functions and their localization into different, though closely neighboring, cortical regions (with the exception of some of the so-called postural movements—"Einstellungsbewegungen"—which have recently been discovered to be initiated in the postcentral cortex; see Graham Brown, Vogt, 1919, Foerster, 1927). Thus in discussing the above question Holmes (1927) states "that the sensory area lies entirely behind the central fissure," and that it "certainly extends over the whole of the postcentral gyrus, over the greater part of the superior parietal lobule, and probably on to the anterior part of the supramarginal gyrus"; equally so, according to Goldstein (1927), the anterior limit of the postcentral granular type of cortex as found by Brodmann and Economo-Koskinas is identical with the anterior limit of the somatic sensory region. The most important zone of that region, according to the dualistic conception, should correspond in the human brain with the posterior lip of the sulcus centralis, although the remainder of the postcentral region and a portion of the parietal region also must have a share in the cortical sensory processes. Physiological investigations (Bartholow, Grünbaum-Sherrington, Mills-Frazier, Vogt, Jolly-Simpson, Cushing, Berger, Lewandowsky-Simons, Leyton-Sherrington, Krause, Valkenburg, Foerster, Mankowski, *et al.*; see Bechterew, Vogt, Monakow, Bergmark, Ariens Kappers, Graham Brown) and clinical and pathological observations (consult Bergmark, Bolton, Monakow, Piéron, Foerster, Kleist, Graham Brown, Goldstein, Holmes, Wilson, Mills) contributed mainly to this solution of the dispute. With the sole exception of cortical cytoarchitecture and myeloarchitecture (Betz, Campbell, Brodman, Vogt, Economo-Koskinas, *et al.*), anatomy has played a comparatively negligible rôle here. Besides being less numerous, anatomical investigations have not been able to give such striking nor apparently such conclusive results as have physiological studies or those in the realm of pathology. Moreover, the scattered anatomical studies, and those few clinical observations, which indicated for the somato-sensory area a much more extensive region of the cortex than the narrow strip immediately behind the sulcus centralis, have on the whole been ignored. The anatomical evidence adduced by Probst (1906), Roussy (1907), E. Sachs (1909) and Wenderowicz (1915), to mention only the most important, showed clearly that not

only does the postcentral convolution receive thalamic fibers, but the precentral convolution as well; though unfortunately in some of these studies an indiscriminate inclusion of other afferent systems into the somatic sensory system led to almost the entire cerebral cortex being accredited with thalamic representation. In numerous publications Flechsig (1894, 1895, 1908, 1920, 1927) also attempted to establish the termination of the thalamo-cortical radiation both in the precentral and in the postcentral convolutions without, however, influencing appreciably the current trend toward the dualistic conception. Flechsig's findings lost power by his own indecision, for in one place he speaks of both central convolutions as the terminal region of the thalamo-cortical radiation, while in another he seems to refer primarily or perhaps exclusively to the postcentral region. Nor was this state of affairs changed by Ramón y Cajal's discovery of the termination in the precentral cortex of exogenous fibers which he declared to be of thalamic origin, for Ramón y Cajal made the mistake of denying altogether the existence of such fibers in the postcentral cortex (1909-11, vol. 2, p. 639); E. Sachs arrived at a similar conclusion in his experiments. The work of some modern investigators, for example, Meier-Müller (1919), Tsunesuke Fukuda (1919) and Minkowski (1923-24), as well as earlier studies of Monakow (1895, 1914, p. 257), Anton-Zingerle, Quensel (1906, 1910), Mingazzini (1913, 1914) and Rutishauser, made at least probable a direct connection by afferent fibers between the anterior portion of the thalamus and the cortex of the frontal lobe; but this work was also ignored, perhaps because other investigators (R. A. Pfeifer, 1920) described the thalamo-cortical radiation as reaching the postcentral region only. There seems to have been a feeling that results which opposed a strictly dualistic viewpoint were due to errors (Horsley, 1909, was thus reproached by Bolton, 1911). In the remarkable physiological investigations on monkeys of Minkowski (1917, 1923-24) and of Dusser de Barenne (1924, 1925) a wider cortical region than the postcentral was found to be concerned with sensation, namely, the postcentral, the parietal, and the frontal (precentral) region as far as the arcuate sulcus. But the arguments brought forward by Dusser de Barenne were regarded as insufficient, and although some concessions were made (according to Foerster, 1925, 1927, the precentral region is an "accessory sensory field" with respect to the "main" postcentral field; see also Ariens Kappers, 1921, 2, p. 1201), the concept of the participation of the precentral cortex in the sensory function was denied (Holmes, 1927). This appeared

justifiable since in none of the experiments performed with conscious subjects were any sensations felt when the precentral cortex was stimulated (Cushing, Valkenburg, Berger, Foerster, Mankowski; the only exception I have found is an observation of Ransom's and of Cushing's, wherein the sensation of motion was recorded although no actual movements were observed). Yet it is difficult to believe that all those results which contra-indicated the restriction of the sensory function to the postcentral region were due to faulty technique or to erroneous interpretation, especially when one compares the large dimensions of the thalamus and the small size of its alleged cortical "representation" (Brodmann's field 1, 2, and 3; compare also Monakow, 1914, p. 252). At any rate the problem of the exact relation of the cortical "sensorium" to the "motorium" apparently deserves a thorough re-study, for it must be admitted that the anatomical investigations of Probst, Roussy, *et al.*, were not carried out with sufficient care, or that in experiments and in pathological cases where the thalamo-cortical radiation degenerated, the visual, the auditory, and possibly other systems were erroneously included within it (Probst, Roussy), or the somatic sensory fiber system was only partly interrupted (E. Sachs), or possibly part of the degenerated fibers had disappeared (Wenderowić). On the other hand, in scarcely any of the physiological experiments involving cortical destruction was the injury strictly confined to the precentral cortex; hence an accidental injury or perhaps only an indirect impairment of the somato-sensory afferent path (because of its position near the precentral cortex) might have occurred; for, of course, this path might conceivably enter the post-central cortex exclusively. A definite decision concerning this is impossible, for our defective knowledge of the exact course and termination of the thalamo-cortical radiation renders adequate anatomical control of such physiological experiments scarcely possible. Thus we see that the old question of whether the somatic sensory cortex and the motor cortex are two separate regions or perhaps one common region, a "senso-motorium" of Munk and Exner, or possibly a more highly organized, composite sensory-motor organ, cannot be regarded as answered definitely in favor of the dualistic conception, in spite of the popularity of the latter among modern neurologists. Nor can the criteria of students of cortical cytoarchitecture and myelo-architecture be accepted as decisive, as is claimed (Betz, Brodmann, Campbell, E. Smith, Vogt, Bolton, Mauss, Nafias, Economo-Koskinas, Goldstein). It is true that the precentral and the postcentral regions

differ considerably in the shape, size, and arrangement of their cells and, somewhat less markedly, in their intracortical fibers. But the conclusion which follows from Meynert's formula that only those cortical regions which possess a well developed inner granular layer ("Koniocortex" of Economo-Koskinas) are the receptive fields of the hemisphere must be regarded as an assumption as yet without definite confirmation. (The inner granular layer as a sole criterion of the receptor function of a certain cortical area was rejected by Vogt, 1911; compare also Economo-Koskinas, p. 237-9, 542). The somatic sensory function, in some respects in contradistinction to the visual, must be regarded as a complex process. Hence, it is a priori possible that besides the forms of sensation requiring the granular cortex of the postcentral type, other forms of sensation may co-exist which are localized in the agranular cortex of the precentral region. Moreover, the granular cortex extends over the parietal lobe, and it may justly be asked how far the parietal cortex also has its share in the somatic sensory function. (Consider the physiological experiments with conscious subjects performed by Foerster, 1927, and by Mankowski, 1929.) Also, as pointed out by Vogt, granules are not entirely absent from the precentral cortex but are only more diffusely distributed therein. (Compare also Economo-Koskinas, pp. 269, 303.) These contradictory results of anatomical, physiological, and pathological investigations may suffice to show the vagueness of the arguments on which the present dominant belief in a complete, or nearly complete, separation of the somatic sensory from the motor function in the cerebral cortex is based (at least in so far as the precentral region is concerned). Especially does the evidence against any receptor function whatever on the part of the precentral cortex appear inadequate. It would appear that this question can be settled satisfactorily only by establishing upon anatomical evidence whether or not the thalamo-cortical radiation terminates in the precentral cortex, as justly pointed out by Minkowski. (See also the interesting views on the relation between the cortical "sensorium" and "motorium" expressed by Ariens Kappers, 1921, 2, pp. 1201 ff.)

In the second afferent fiber system of the forebrain cortex, the *auditory system*, there is scarcely less uncertainty. Here, too, the question whether the "primary" or projectional auditory cortex is a small, well defined area, or whether it extends over a considerable portion of the temporal cortex, does not seem to have been settled satisfactorily. The view formerly accepted, that it extends over a large

portion of the temporal lobe, or perhaps occupies the entire temporal lobe (Wernicke, Monakow), has gradually receded before the belief in a narrow and perhaps sharply delimited area, confined by some investigators to the superior temporal convolution (Ferrier-Turner), by others to the transverse temporal convolution of Heschl (Probst, Quensel, Wenderowič), and by yet others reduced to a portion of the anterior transverse temporal convolution (Flehsig, 1908, 1920, 1927; Henschen, 1918, 1919; R. A. Pfeifer, 1920). Such a reduction of the auditory projection area, the cortical representation of the papilla basilaris of the cochlea, to a mere fraction of the temporal cortex is clearly in disagreement with the delimitation made by students of cytoarchitecture and myeloarchitecture (Brodmann, Mauss, Vogt, Economo-Koskinas, Beck). The relation between fiber anatomy on the one hand and cytoarchitecture and myeloarchitecture on the other with respect to the "primary" region of the auditory cortical sphere is the reverse of the situation which we have described with respect to the somatic sensory cortex. Whereas cytoarchitecture and myeloarchitecture show that the somatic sensory cortex is smaller than is claimed by fiber anatomy, the auditory projection cortex of the students of cytoarchitecture and myeloarchitecture is much larger than is admitted by the students of fiber anatomy. Nor have clinical and experimental investigations clarified this problem except to show the approximate location of the auditory "centre" (which, incidentally, has been done in a much more precise way by the anatomical studies of Flehsig, Vogt and R. A. Pfeifer); this is true of the recent clinical investigations (e.g., Kleist, 1928) which claim a multiple cortical representation of the cochlea (a conception similar to Monakow's and Goldstein's view on the cortical projection of the retina, especially of the macula), likewise of those of Börnstein (1930) which lack the necessary anatomical control, and of the experimental anatomical investigations of Minkowski (1923-24). Clearly the opinions of various investigators concerning the extent of the auditory projection cortex are contradictory: the cortical area receiving direct impulses from the subcortical cochlear nuclei is either a small, sharply delimited region, or it occupies a wide portion, or perhaps the entire temporal lobe. In this respect the myelogenetic method does not give a full guarantee that nothing besides the anterior transverse temporal convolution belongs to the auditory projection cortex in the adult brain. Of the results of cytoarchitectural investigations, the statement made with reference to the somatic sensory "Konicortex" holds true.

Physiological and clinical studies present so many sources of error that the conclusions drawn therefrom must be accepted with reserve; in the present state of our knowledge any physiological investigation is hampered by our ignorance of the situation of the auditory projection cortex in lower primates. Yet the problem of whether the auditory projection cortex is a small area with sharp boundaries or, on the contrary, one which extends over a considerable portion of the temporal cortex or even over that entire lobe, is of fundamental importance for all further understanding of the physiology, psychology, and pathology of auditory performances, including the highest processes which manifest themselves as speech, understanding and reproduction of music, and understanding of numberless biologically important irregular acoustic stimuli of everyday life (noises). It is evident that an attempted explanation of these higher auditory processes and localization thereof into special portions of the auditory cortex will have, at most, only an approximate value or will remain doubtful as long as the basic questions mentioned above are not definitely settled. (Compare the uncertainty as to the finer localization of various forms of aphasia and the confusion in its interpretation in Pick, Monakow, 1914; Head, 1925, vol. 2, pp. 468, 474, 498; Goldstein, 1927, p. 759, etc., but see also Hensehen, 1918, 1919, 1927; Isserlin, Niessl von Mayendorf, 1930, *et al.*) The experimental anatomical method seems well adapted to help solve these problems and to determine at least the comparatively gross features of the central auditory mechanism. Everything here depends on the formulation of the problems, on the choice of the material, and very considerably on the technique. The first question to be settled is the exact origin, course, and termination of the central portion of the auditory afferent path. If the auditory radiation after the destruction of the internal geniculate body be found to terminate in a well delimitable, small cortical area, this will permit the conclusion that there is, indeed, besides the auditory projection cortex another portion of the cortex to which functions higher than mere reception of auditory impulses must be attributed. The conviction that only a small portion of the temporal cortex serves as a "gateway" for all cortico-petal auditory impulses would be justified if in a suitable experiment all suggested afferent pathways of the temporal cortex were severed, and only a single degenerated afferent fiber system terminating in a small area were actually found. If the auditory radiation, on the contrary, were found to spread over the whole temporal lobe this would unavoidably

force us to the conclusion that the whole auditory cortex has the receptive function and is at the same time subservient to all the higher integrative or associative processes of audition. In the latter case there would hardly exist any local or areal differences in auditory performance; at any rate the diversity of the central auditory processes would have to be explained in quite a different way.

As to the third main afferent system of the cerebral cortex, the *visual system*, especially the central portion of the visual path (visual radiation) and its cortical termination, the majority of contemporary authorities adhere to the conception first formulated by Wilbrand, Henschen, and Flechsig. According to this, and in opposition to Monakow and other decentralists (Hitzig, Gudden, Loeb, Luciani, Goltz, Déjérine, Edinger, Bernheimer, Wehrli, S. I. Franz, Stauffenberg, Winkler, Goldstein, *et al.*; see also Economo-Koskinas, p. 655), the central visual path has its only subcortical origin in the external geniculate body of the between-brain, forms a definite fiber system of the hemisphere, the so-called external or lateral sagittal stratum of the parieto-occipital lobe (H. Sachs), and has its exclusive cortical termination in the striate area of Elliot Smith, field 17 of Brodmann, the OC of Economo-Koskinas. Besides, the striate area represents a faithful copy of the retina. It was the patient work of Flechsig, Henschen, Wilbrand, and also of other numerous anatomists (Hösel, Probst, Niessl von Mayendorf, La Salle Archambault, Meyer, Rönne, Brouwer, 1917 and 1930; Wenderowicz, R. A. Pfeifer, 1925 and 1930; Putnam, *et al.*), corroborated by experiments (Munk, Minkowski, Bechterew, Brouwer-Zeeman, Overbosch, Brouwer-Heuven-Biemoed, Heuven, Foerster, 1929, *et al.*) that established this opinion which has now had confirmation in the numerous experiences of the World War and later (Uthhoff, Marie-Chatelin, Holmes-Lister, Saenger, Best, Holmes, Lenz, Chatelin, Souques, Kleist, Axenfeld, and especially Foerster, 1929, *et al.*). We must admit, however, that all this accumulated evidence for the existence of a single, definite central visual path terminating in a single, sharply delimited cortical area identical with the area striata and apparently confirming the conception of the fixed projection of the retina upon the cortex is by some investigators by no means regarded as conclusive and unassailable. (The anatomical control of the numerous pathological cases is quite scanty.) This is well illustrated by views expressed recently by Goldstein (1927, pp. 600, 729). Goldstein not only adheres to Monakow's ideas of a threefold subcortical origin of the visual radiation

and of a multiple cortical representation of the retina including the macula, according to different architectural and functional principles (ideas at present regarded by the majority as obsolete); he even doubts the existence of any finer projection of the peripheral visual receptive surface upon the cerebral cortex. There should be, Goldstein thinks, no reason for accepting a strict correspondence between each of the retinal segments and those of the striate area. He believes that in the visual system "only a relatively roughly delimitable projection has been evidenced and can be proved." It is true that contrasted with the abundance of pathological and clinical observations on visual disturbances in cases with various injuries of the occipital lobe, very little investigation of the visual radiation and visual cortex in man by anatomical methods, especially by secondary degeneration—which would really clarify the entire central visual mechanism—has been made. Furthermore, a systematic experimental anatomical investigation of the internal arrangement of the visual radiation in higher mammals (primates) is conspicuous by its complete absence. It is especially remarkable that no attempts have been made hitherto to analyze the finer organization of the central portion of the visual apparatus by experiments with monkeys (the peripheral portion was studied by Brouwer and Zeeman).¹ Some hints in this respect were obtained by anatomical studies of human pathological material with more or less limited injuries (Henschen, Quensel, Monakow, Zingerle, Winkler, Brouwer, Niessl von Mayendorf, Putnam, *et al.*). On the other hand, studies of normally stained preparations of human hemisphere (Flechsigs, Henschen, Probst, Niessl von Mayendorf, La Salle Archambault, Brouwer, Putnam, R. A. Pfeifer), valuable as they were for the comparatively gross features of the visual radiation, proved insufficient for the explanation of its minute, internal organization and in particular of the projection of various quadrants of the retina and especially of the macula upon the cerebral cortex (see Flechsigs, 1927, p. 93). It seems certain, therefore, that a thorough and systematic study of the central portion of the visual apparatus in respect to its peripheral portion after the manner of Brouwer and Zeeman and their collaborators, is required before any clear view can be attained as to how and where the various retinal quadrants are exactly projected and how they are represented in definite segments of the visual radiation and in the visual cortex. The number of detailed

¹ In this respect much has been gained from the recent experiments of Brouwer and Heuven.

problems of the central visual apparatus still remaining unsolved is considerable. To date it is not known precisely where the most important portion of the visual radiation—the macular path—lies, and whether the “macular bundle” is a small or, on the contrary, a considerable portion of the visual radiation, and how and where it reaches the macular cortex. Another problem has to do with the determination of the shape, size, and position of the individual segments of the visual cortex supplied by individual bundles of the visual radiation and in particular their shape and position in the macular and in the perimacular portion of the cortex. A further question requiring a clear-cut answer is, whether or not a portion of the visual radiation, especially macular fibers, undergoes a second decussation or re-crossing through the corpus callosum (“fasciculus corporis callosi cruciatus” of R. A. Pfeifer). Such or a similar decussation and consequently the existence of a double or bilateral cortical representation of each total macula in both hemispheres has been presupposed by some investigators (Heine, Wilbrand, Lenz, R. A. Pfeifer, Foerster) in their attempts to explain the preservation of “central” or macular vision in cases of hemianopsia. And finally, the general architectural principle according to which the entire visual system is organized must be elucidated—certainly a problem of paramount importance for the psychology, physiology, and pathology of vision. We refer to whether the individual small fiber fascicles which form the visual radiation supply small segments of the visual cortex, each bundle supplying only its own segment, without intermingling or overlapping, as postulated by the strict localistic conception; or whether, on the contrary, no such strictly regular or “spatial” arrangement with absolute separation and isolation of the individual bundles exists, these probably terminating in “diffuse” way or with mutual overlapping, as claimed by the opponents of the localistic conception (not to mention the purely “dynamic” concept of the “Gestalt” psychologists). If it were possible after injury (isolated or not) of the subcortical visual nucleus or of the visual radiation to show anatomically that (a) all fibers of the visual radiation terminate in the striate area exclusively, and (b) that each definite, individual fascicle of the visual radiation supplies a definite, well delimitable portion of the visual cortex and only that, the dispute between the localists and their opponents could be considered finally settled in favor of the localists. If, on the other hand, the visual apparatus is not organized according to the principle of localization but is in its gross relation

to the cerebral cortex, as in its internal organization, "diffusely" arranged, and if there are several distinct, independent portions of the visual radiation, and the cortical representation of the retina together with that of the macula is multiple, as claimed by the decentralists, one would expect this to be demonstrable by experimental anatomical methods. In this important question only an opinion based on facts controllable and measurable by exact methods can be accepted. The fact that opinions on the visual apparatus still fluctuate and are contradictory, unquestionably a consequence of insufficient anatomical knowledge, is exemplified by the explanation of the preservation of the "central" or macular vision in cases of hemianopsia given recently by Wilbrand (1925, 1926). Although there should be, according to Wilbrand, a fixed or stable projection of the retina upon the cerebral cortex, this in some sense should not be the case in the macular portion of the visual radiation and of the visual cortex (exactly in that portion where the most rigid observance of the "principle of localization" could justly be expected, if that principle exists at all in the visual system; here I call attention to the very minute projection of the individual retinal segments upon the external geniculate body, belonging in all probability to the macula, found in the cat by Overboeseh, 1927). According to Wilbrand, each macula should be projected in its totality upon the cortex of both hemispheres, wherein each of the macular sensitive elements, each cone, would perhaps be represented in both hemispheres. Such a bilateral or double cortical representation of each total macula would explain the preservation of "central" or macular vision in cases of hemianopsia where such a sparing is observed, but would undoubtedly be an obstacle in explaining macular (central, paracentral) scotomata and other cases of hemianopsia where there is no sparing of the "central" vision. A bilateral cortical representation of each total macula would be somehow reconcilable with the strict localistic viewpoint, although, as will be shown later, for anatomical reasons no bilateral projection of each total macula in the above sense is acceptable. Yet in his attempts to explain the sparing of macular vision Wilbrand constructed an additional hypothesis. He supposes a substitution of the function of the destroyed segments of the macular cortex or of the interrupted macular fibers by other portions of the macular cortex remaining normal, since, according to his notion, each macular cortex has to be regarded in some sense as a functional unit, working as a whole. But, as can easily be understood, such a conception of the organization and function of the macular

cortex is nothing short of the renunciation of the localistic conception as regards the most important portion of the central visual apparatus, a conception otherwise eminently and successfully maintained by Wilbrand, and an approach to the views of Monakow, Goldstein and the "Gestalt" psychologists on a multiple or a "diffuse" cortical projection of the macula and of the entire retina, acting as a "dynamic" whole.

The few examples mentioned in the foregoing pages should suffice to illustrate the uncertainties existing even in respect to cardinal features of the organization and function of the afferent systems of the cerebrum. At the same time this should be ample justification for the present experimental studies.

CHAPTER III

MATERIAL AND METHODS

The above mentioned and many other deficiencies and contradictions in our knowledge of the central nervous mechanisms and the belief that only palpable and reliable data, so far as these can be obtained, can solve the discussed problems induced me to attempt to attack by experiment some of the more important problems of the fiber anatomy of the forebrain, and thus of the functions of certain fiber systems and cortical regions, or areas, connected with these. There can be no doubt as to the advantages of experimental anatomical methods of investigation provided a suitable procedure is chosen and the application of the method is sufficiently accurate and the interpretation of the results sufficiently critical. Attention has already been called to the relative value of most of the arguments upon which the prevalent modern views on brain organization and function are founded. Mention has also been made of the slender exact anatomical data on the afferent fiber systems of the fore-brain. Nowhere have we detailed and exhaustive descriptions of these systems supported by sufficiently numerous and accurate illustrations. Most of the evidence hitherto used has been derived from physiological and pathological observations without adequate anatomical control, or this control was carried out in a superficial, summary way. It is also true that there exist only a few dependable anatomical investigations on the central portions of the somatic sensory, auditory, and visual systems, none of them giving a full and complete analysis of the finer, internal or functional organization of the fiber systems in question (in man and in primates). No satisfactory experimental anatomical investigation of the three main afferent fiber systems of the cerebral cortex from their subcortical origin to their cortical termination has as yet been undertaken in primates;¹ all data has been derived from normal human and mammalian or from pathological human material, the latter, because of the extensiveness of the destruction, being usually unsuitable for any finer analysis. It will be admitted that the controllable results of experimental anatomical inquiries will be much more persuasive than deductions made from physiological, clinical,

¹ The only exception is the visual system, thanks to experiments of Brouwer and Zeeman, and of Heuven.

and pathological studies which are often ambiguous, indispensable as they may be. And lastly, mention must be made of the scant applicability of Weigert's and similar methods of staining, applied almost exclusively in previous investigations of human pathological material, a fact which, though not admitted by many investigators, accounts for the limited results of most of these studies.

The present plan involves at first a systematic investigation of the three main afferent pathways of the cerebral cortex: the somatic sensory, the auditory, and the visual. The next step, especially after the projection areas of the cortex of the above mentioned afferent paths are determined, will be to study the manner of spread or diffusion of the respective impulses from each of the projection areas or "gateways" of the hemisphere to other areas and regions of the cortex. The third objective will be the study of the interrelationships of various areas and regions of the same and of the opposite hemisphere as well as of their efferent connections. It will be granted that this extensive plan is costly in time and effort, yet sufficient progress has now been made to warrant publication of the conclusions reached with regard to the afferent paths. The conclusions rest on repeated re-examination and analysis of the preparations. A detailed description of experiments on afferent paths, with due consideration of previous investigations and with conclusions important for physiology, pathology, and psychology will, therefore, be given in the present monograph. In a few places the results of other original experiments on the association, callosal, and efferent fiber systems will be mentioned but only when they stand in close relation to the investigated afferent paths.

To obtain results applicable to human physiology and pathology, the present experiments were carried out on monkeys (*Macacus rhesus*, except in Experiment V-A, V-B, V-D, and V-E where a Java monkey was used). As far as the afferent paths are concerned, my attempt was to interrupt the fiber systems in question either at their diencephalic origin or close to it. Thus I hoped to bring the investigated afferent paths to a partial or a complete degeneration, avoiding at the same time as far as possible other fiber systems. It was my intention to trace the secondarily degenerated afferent fibers to their respective terminations in the cortex and to study: (a) the extension or the boundaries of the "primary" or projection areas of the cortex, (b) the finer relation of the afferent fibers to the cortex, and (c) the internal arrangement of the three investigated afferent paths. The method

used in all the present experiments was that of Marchi which, in my experience, is far superior to any other method, particularly in experimental work on the fiber systems. If properly applied, this method gives clear pictures of black degenerated fibers contrasting with the green or yellowish color of fibers remaining normal, a contrast reproduced in the accompanying illustrations. To obtain sure orientation concerning the extent of the supplied cortical areas or regions, I sketched in various positions each of the operated brains as soon as removed from the skull. The brains were hardened in Müller's fluid without the addition of formol and further divided in the usual way into thin slabs (1-2 mm.). Each slab was shown in the orientation drawing and designated with a number corresponding to its position in the brain. After staining in abundant Marchi's solution and thoroughly washing in running water, the slabs were once more put together in their natural order, three to five slabs at a time, hardened and dehydrated in pure acetone (to which burned copper sulphate was added) for two to three hours in the thermostat, thoroughly washed in absolute alcohol (to remove the acetone), put into thick celloidin (10-15 per cent), mounted upon wooden blocks (with cork underneath), submerged for half an hour in pure chloroform till the celloidin became hard enough, transferred to 80 per cent alcohol, and cut into continuous series. The sequence of numbers of the sections corresponded with the slab sequences in the drawings. (On Marchi's method consult Lange, Gehuchten et Molhan, Spielmeyer, Schmorl, R. Krause, and Vogt, 1928, p. 472.)

Since the series of all operated brains were continuous, an accurate delimitation of the cortical areas or regions supplied by the degenerated afferent paths, or by portions thereof was achieved; in other experiments the areas supplied by association and callosal fibers were delimited. In studying the series, attention was paid to minute details as well as to the main features of various fiber systems.

In addition to the study of various fiber paths by means of Marchi's method, a number of experiments were performed on the *Macacus Rhesus* and on the Java monkey according to Nissl's method: the "Primary Irritation of Cells or the Retrograde Degeneration" of the nerve cells whose axis cylinders were interrupted. (For the description of the method see Nissl's article in R. Krause's *Encyclopaedia*, p. 1642.) These experiments deal with various problems concerning the finer or "internal organization" of the visual system. It was hoped that by making small injuries of various sizes and localities in

the striate area, and in such a way damaging the terminal branches of the particular bundles of the visual radiation, sufficient changes of the nerve cells in the lateral geniculate body would be obtained. This would make possible not only a satisfactory knowledge of the projection of various segments of the mentioned body—and thus of the retina upon the striate area, and so forth—but would as well prove or disprove the assumption of a structural basis for the preservation of the “figures” in visual acts. (Compare Chapters XVI and XIX.) In our experiments the Nissl-Spielmeier’s method of staining with thionine blue was used in most cases and it proved to be satisfactory, giving clear differences between normal and degenerated cells; only in one instance was the method of Van Gieson used, which, though it gave fairly good results appeared for our purpose decidedly inferior to Nissl’s method. The camera lucida of Zeiss was used in preparing the illustrations.

Conclusions regarding the three paths investigated were obtained from eleven experiments; other results from experiments not reported in detail here, altogether twenty-five single experiments performed on twenty-one brains, are also briefly mentioned. The description of the afferent paths in the present report is as complete as possible, including all finer details, and the illustrations are made as faithfully as can be, to enable the reader to form his own independent judgment and conclusions. The accompanying illustrations—all drawn by the author himself—are actual drawings of the sections made with the help of the camera lucida of Zeiss and Leitz, the details representing the degenerated fibers being combined, as a rule, from a few closely neighboring sections. Preference was given to drawings since the details of photographs when reproduced usually lose greatly in distinctness. The terminology of the thalamus is that used by Marburg (1927).

PART I
SOMATIC SENSORY SYSTEM

CHAPTER IV

THALMIC TERMINATION OF AFFERENT SOMATO-SENSORY FIBER TRACTS. INTRATHALAMIC FIBER SYSTEMS

Four of the experimental injuries reported in the present monograph involved the thalamus or the adjacent internal capsule causing various intrathalamic fiber systems to degenerate (for the description of lesions see Chapter V). These fiber systems were:

1. Ascending fiber tracts from the lower centers of the neuraxis.
2. Fibers of thalamic origin which enter the basal nuclei and the cerebral cortex.
3. Fibers originating from the cerebral cortex and, entering the thalamus; these either terminate here or merely traverse it on their way to the midbrain.
4. Fibers which originate and terminate in the thalamus. In a restricted sense, only the latter fibers are validly intrathalamic.

On the thalamic termination of fiber tracts ascending from lower levels of the neuraxis the present experiments, naturally, can give only general information. Nevertheless, they throw new light upon the subject (Experiment II especially). From the thalamic injury which occupies approximately the position of the ventral portion of the external medullary lamina (figs. 50 and 51) numerous degenerated fibers in dense fascicles ascend dorsalward into the lateral nucleus, crossing at right angles the emerging horizontal thalamo-cortical fibers (figs. 48, 50, 51). These fibers, of different size though mostly of large caliber, evidently belong to the incoming fiber tracts from the lower segmental regions, that is, to the medial fillet (figs. 50, 51), to the cerebello-thalamic tract (fig. 48), and perhaps also to the spino-bulbo-thalamic tracts. These ascending intrathalamic fibers gradually decrease in number and in size toward the dorso-lateral nucleus, and usually disappear before attaining the upper half of the dorso-lateral nucleus. It would, accordingly, appear as though only the ventro-lateral nucleus and the lower half of the dorso-lateral nucleus receive these afferent fibers. Yet it is to be remembered that these fibers lose their myelin sheaths before entering their terminal ramifications. For

this reason and for the reason that in many sections degenerated fillet fibers have been traced to the most dorsal corner of the dorso-lateral nucleus, it is much more probable that the afferent sensory tracts attain all parts of the lateral nucleus including its dorsal portion close to the zonal stratum. Still another feature, however, seems important in understanding the mode of distribution of afferent sensory fibers within the thalamus. Figures 50 and 51 suggest the fairly regular course of the bundles of incoming fibers, arranged in semicircles parallel to the slightly bulging lateral contour of the lateral nucleus. They mix little with one another and change their course little. Besides, the stream of afferent fibers occupies almost the entire width of the lateral nucleus between the external and the internal medullary lamina and is most dense midway between them. This observation suggests that the afferent thalamo-petal tracts occupy not merely a narrow zone beside the external medullary lamina, as still believed by some investigators (Ingvar, 1925), but are really distributed to the entire lateral nucleus of the thalamus. Moreover, the gradual disappearance of all afferent fibers within the thalamus and their course, different from that of the thalamo-cortical fibers, makes it also appear fairly evident that there is no basis for accepting the existence of a fillet system continuous to the cortex; for, all afferent sensory fibers from lower regions end within the thalamus. With respect to the spino-thalamic tract, this was further substantiated by an experiment with Macacus not further reported here.

The present experiments show numerous other degenerated fibers merely traversing the thalamus in their course from the hemisphere to lower regions of the neuraxis. Such fibers are particularly conspicuous in the ventral and ventro-lateral portions of the pulvinar (figs. 34-36, 96). They traverse this thalamic region in more or less horizontal, thin bundles containing fine as well as medium sized fibers, and a few coarser ones, all forming a fairly dense meshwork condensed in a few spots to thicker bundles. Eventually they all converge toward the inner border of the pulvinar where they form a single trunk connecting the pulvinar with the anterior quadrigeminal body, called the brachium or arm of the superior colliculus (figs. 36, 96). In Experiments I and XV (the latter not reported here in detail), where the occipital lobe or the angular convolution was destroyed these fibers degenerated partly or entirely, demonstrating their cortical origin and their cortico-fugal character. Within the superior colliculus, these efferent fibers form mainly the superficial

medullary stratum, less the intermediate and zonal strata. The deep medullary layer of the superior colliculus and central gray substance around the Sylvian aqueduct is not reached by this fiber system. Nor is there evidence that these fibers cross either to the opposite superior colliculus or reach the inferior colliculi. The tract in question is the occipito-parietal cortico-tectal fiber system for oculo-gyric and other eye and head movements. The degeneration in Experiment I of this entire tract toward the superior colliculus speaks against the latter nucleus being a subcortical visual center for cortico-petal impulses. (Compare also: Visual System.)¹

Another small fascicle of fine fibers degenerated in Experiment II (figs. 52 and 53). From the external geniculate body it passes alongside the internal geniculate body and through the pulvinar it reaches the upper strata including the stratum zonale of the superior colliculus, losing fibers which appear to terminate in the posterior nucleus of Monakow situated between the two geniculate bodies. Here, however, it cannot be decided whether these fibers are special direct fibers from the optic tract, or collaterals of these, or perhaps axis cylinders of neurons situated in the external geniculate body.² It is more than probable that these superficial fibers which degenerated toward the midbrain, whatever they may be, represent the tract for pupillary light reflex (Ingvar, Brouwer-Zeeman; see also Visual System in this work).

A number of degenerated fibers found in the thalamus may be of a cortical origin. They descend from the hemisphere to the entire lateral nucleus of the thalamus in its posterior segment, and to the ventral portion of the pulvinar (fig. 66), while none were seen to enter the dorsomedial region of the latter. These fibers are fairly numerous and of various caliber, some being fairly coarse. (See also Chapter V, Experiment III.)

In a few instances fine blackened particles and "dust" found within the thalamus can be interpreted as local short association fibers. The dorsomedial region of the pulvinar, especially where it was possible to exclude the presence of descending cortico-thalamic fibers lends itself to this interpretation (fig. 36).

¹ Another experiment not reported here in full, where only the fields 18-19 of Brodmann were damaged, substantiates this. No such fibers descend from the field 17, or the area striata.

² This latter possibility has to be discarded in view of the fact that the lateral geniculate body degenerates completely after the complete destruction of the ipsilateral striate area, as the Experiment V-E shows (see also Experiment V-D).

It has not been possible to ascertain whether any fibers of the medial fillet reach the medial and the anterior nucleus of the thalamus, though some having a fine caliber enter the internal medullary lamina, being more numerous in the ventral portion of that lamina, from which they might enter the medial nucleus.

CHAPTER V

ORIGIN, COURSE, AND TERMINATION OF SOMATO-SENSORY
THALAMO-CORTICAL AND THALAMO-STRIATE FIBERS

In four of my experiments, as far as the somatic sensory system is concerned, I attempted to interrupt the thalamo-cortical radiation by injuring the thalamus or by cutting the radiation itself close to the thalamus (for Visual and Auditory central paths investigated in the same cases, see corresponding chapters). This was achieved in Experiment I almost entirely by an intrathalamic lesion (*L* in figs. 28-31, 33-36); in Experiment II the thalamo-cortical radiation was interrupted chiefly within the internal capsule in the immediate vicinity of the thalamus (*L* in figs. 48-51), and partly by an intrathalamic lesion (figs. 50, 51); while in Experiment III and V-A a portion of the radiation was interrupted within the internal capsule exclusively (*L* in figs. 5 and 66). In Experiment I a considerable part of the radiation degenerated. In Experiment II probably a majority, if not all of the fibers of the thalamic radiation degenerated; while in Experiment III only the posterior or caudal half of the radiation, and in Experiment V-A only the intermediate segment of the radiation degenerated.

The primary object of these experiments was to produce as complete as possible a degeneration of the entire central portion of the somatic sensory path and, using Marchi's method, to determine the "minimal" cortical region of the hemisphere supplied by fibers of thalamic origin. Next it was intended to determine the origin, course, and termination of parts of the thalamo-cortical radiation as well as to delimit cortical areas where such individual bundles of the radiation terminate. The third object of the investigation was to study minute relations of the afferent somato-sensory fibers to cortical structures.

EXPERIMENT I

In Experiment I a lesion was produced by plunging a small Graefe's knife into the spot indicated in figure 1 as a small dotted area in the lowermost part of the angular convolution, close to the sulcus occipitalis inferior. The instrument was directed mesially and

at the same time oralward, reaching the thalamus from behind in order to avoid the internal capsule and the corpus callosum (figs. 38, 37, 36, 35, 34, 33, 31, 30, 29, 28). By using a single cortical entrance and directing the instrument according to carefully laid plans, the destruction of cortex and subcortical white substance of the parietal lobe was minimized (see also chapters on the Visual and Auditory System).

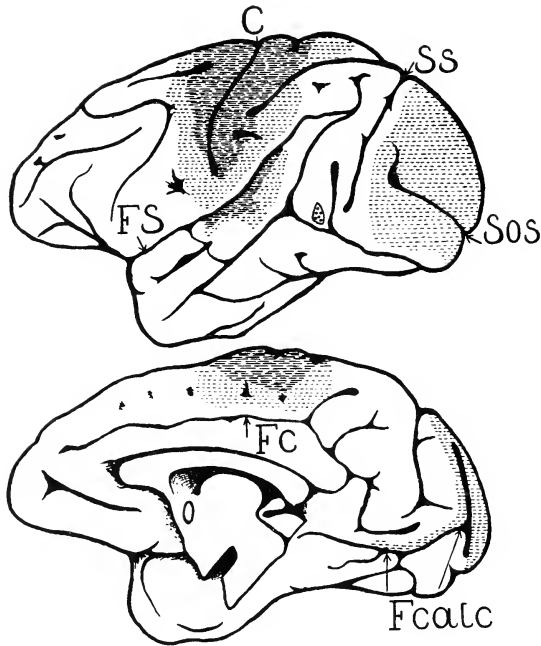


Fig. 1, Experiment I. External (upper figure) and internal (lower figure) face of the monkey's hemisphere showing the location and extent of the three projection regions of the cerebral cortex found in this experiment (shaded areas). Somatic sensory region on both sides of the central sulcus (*C*) and above the fornicate sulcus (*Fc*); auditory region below the Sylvian sulcus (*FS*); visual area behind the simian sulcus (*Ss*) and along the calcarine fissure (*Fcalc*). Differently shaded areas indicate rough differences in the number of afferent fibers. The small dotted area represents the superficial lesion through which the knife was introduced into the substance of the hemisphere. Superior occipital sulcus, external calcarine sulcus (*Sos*). (Compare figs. 26-43.)

This injury (*L* in corresponding figures) directly destroyed the following parts of the thalamus: the pulvinar which is either destroyed or greatly separated from the hemisphere (figs. 34-36), further a

part of the dorso-lateral nucleus, a part of the ventro-lateral nucleus, and also a part of the central nucleus (Luys) of the thalamus (figs. 28-31, 33), leaving the remaining regions of the thalamus intact (fig. 27). A part of the external geniculate body, the medial or the internal segment of its posterior "spur," and the internal geniculate body were also directly destroyed (figs. 33-35). The longitudinal extent of the injury occupies more than the caudal half of the thalamus; the injury decreases, however, rapidly in size oralward, leaving the oral segment of the thalamus uninjured (fig. 27). Although its distance usually ranges only 1-2 millimeters from the lateral border of the thalamus and from the internal capsule, the lesion remains everywhere strictly within the thalamus (figs. 28-31, 33, 34), except near the caudal extremity of the pulvinar where the instrument reached the diencephalon (figs. 35, 36). Except in the most oral sections where the lesion barely reaches these fiber layers (fig. 28), even the external medullary lamina and the reticulate stratum of the thalamus remained untouched by the lesion.

In consequence of the injury a large number of fibers forming the thalamo-cortical radiation (*sr* in corresponding figures) degenerated. To some extent they can be followed as separate bundles to their respective cortical terminations. From the pulvinar proper, especially from its dorsal portion, only fine, poorly myelinated fibers arise. Of these, some have been traced to the near-by tail of the caudate nucleus (fig. 35, upper lesion *L*), others through the internal capsule to the putamen and globus pallidus. Scarcely any of these fine fibers reach the cerebral cortex. However, the cortex might be reached by a few fibers of medium size from the ventral portion of the pulvinar.

Fibers originating from the lateral nucleus of the thalamus, mostly of fairly coarse appearance, emerge from every part of it into the internal capsule as a broad stream. Immediately, or within a short space, they turn dorsalward along the dorsal corner of the thalamus toward the upper half of the hemisphere. Their further course and ultimate cortical termination differs depending upon their thalamic origin. Thus, bundles originating in the dorso-lateral nucleus and consisting of thin, medium sized, and numerous coarse fibers proceed for the most part directly upward to reach the uppermost sectors of both central convolutions and the neighboring portion of the inter-hemispheric cortex (figs. 29-31, 33). Other fibers, arising from the ventral nuclear group of Monakow, also mostly of large caliber, pene-

trate the ventral portion of the internal capsule and form there arch-like bundles between the putamen and thalamus. The most lateral of them even pass through the substance of the putamen. On the whole, they form the lateral bundles of the thalamo-cortical radiation which, closely pressed to the claustrum, ascend toward the ventro-lateral (opercular) segments of both central convolutions (figs. 30-34). Accordingly, fiber groups from the uppermost portion of the dorso-lateral nucleus are the most dorso-medial part of the radiation; those from the ventro-lateral nucleus are the most ventro-lateral; the remaining bundles are the intermediate portion. All these fiber bundles together form, in fact, individual "fans" arranged dorso-ventrally. The fans in turn are arrayed perpendicularly and somewhat obliquely with respect to the long axis of the hemisphere, or, in other words, to the long axis of the thalamus. They follow consecutively one behind the other: the most oral fan emerging from the most oral portion of the thalamus, the most caudal (posterior) fan from the most caudal portion, the middle fan from the middle portion. (Compare Experiment V-A.)

Moreover, it is evident that the thalamo-cortical radiation together with the acoustic radiation (*ar* in corresponding figures) arising from the internal geniculate body forms a huge system of diencephalo-cortical fibers wherein the acoustic radiation occupies a most ventral position. The visual radiation (*vr* in corresponding figures), as will be shown later (see Visual System), forms a part of the diencephalo-cortical fiber system only at its beginning within the internal capsule, diverging from the common somato-sensory-acoustic portion of the mentioned system as it approaches the occipital cortex.

Thus, considering only the individual bundles or "radii" of the thalamo-cortical radiation forming the described "fans" there is an uninterrupted chain of such "radii" arranged or segmented both longitudinally and perpendicularly with respect to the long axis of the hemisphere. These radii are, on the whole, at their thalamic origin near one another, and diverge as they approach the cortex.

In certain sections (figs. 30-34) it is even difficult because of their proximity to distinguish ventral bundles originating in the ventro-lateral thalamic nucleus (and perhaps also in the hypothalamus) from the central acoustic path. Only by tracing the further course of the acoustic bundles toward the superior temporal convolution (T_1 in corresponding figures) along the lower lip of the Sylvian fossa (*PS*) and the course of the ventral thalamo-cortical bundles

toward the operculum can they be identified. In the same way that the ventral thalamo-cortical bundles turn lateralward to reach the opercular region (figs. 29-31), the dorsal bundles from the dorsal portion of the middle segment of the dorso-lateral nucleus of the thalamus curve dorso-medially in more rostral planes to reach the dorsalmost segment of the precentral convolution (figs. 26, 27). Ventral bundles, as evident from figures 30 and 31, after crossing the most ventral region of the internal capsule and the triangular field of Wernicke (beginning of the visual path) penetrate in part the caudal portion of the putamen dividing the latter nuclear mass into several islets (*Put* in fig. 32); they finally enter the external capsule where they turn dorsally, ascending here pressed closely to the claustrum and appearing as a thin layer of short oblique fiber segments (figs. 33, 34). The more ventral of these bundles, some of them within the extreme capsule (figs. 31, 33), belong evidently to the central auditory path (others to the anterior commissure).

The course of various bundles of the thalamo-cortical radiation can easily be seen in the accompanying illustrations, in which, also, the most caudal fibers are shown as participating in the formation of the external sagittal layer (stratum) of the parieto-occipital lobe. This will be more evident in the following experiments. (On the cortical region receiving thalamic fibers and on the mode of intracortical termination of these, see corresponding chapters.)

In the accompanying illustrations it can also be seen that all thalamo-cortical fibers, whether arising from the dorsal or from the ventral region of the thalamus, converge, in their ascent through the internal capsule, at a spot close to the dorsal corner of the thalamus (fig. 30). They must all pass through this narrow passage to reach the centrum semiovale situated above, and finally, the cortex. At the point of convergence they can all be easily interrupted by a comparatively small lesion (compare Experiment III and V-A, figs. 5, 66), whereas a small lesion situated below or above that spot or in the thalamus itself will produce, on the contrary, degeneration of only part of the thalamo-cortical radiation. This is due to the spread of the various individual fiber bundles of the radiation when still within the thalamus or in the centrum semiovale above the narrow passage mentioned, and accounts for the smaller absolute number of degenerated thalamo-cortical fibers in Experiment I than in Experiment II, III, and V-A.

The region of the thalamus more extensively destroyed in Experiment I is its posterior and middle third; the anterior (rostral) segment remained uninjured. Accordingly, all thalamo-cortical fibers degenerated in the present experiment must originate in the caudal and middle segments of the thalamus. When considering the region of the cortex receiving thalamic fibers in the present experiment (shaded areas around the central sulcus in fig. 1, see also chapter on Extent, etc., of the Somatic Sensory Cortex), it is evident from the shape of that region, even more so in Experiments III (fig. 3) and V-A (fig. 4), that the fiber bundles of the thalamo-cortical radiation must of necessity be arranged in "fans" placed perpendicularly though somewhat obliquely to the long axis of the hemisphere, in order that each of them may supply a narrow strip of cortex approximately parallel to the sulcus centralis of Rolando. (A similar view on the vertical segmentation of the hemisphere has been expressed by Ch. Jakob and Onelli.) The segmentation of the thalamus and of the whole thalamo-cortical radiation found in the present investigation harmonizes well with the areal differentiation of the cerebral cortex found in cytoarchitectural and other investigations. This arrangement which seems to be especially well marked on both sides of the sulcus centralis (Brodmann's areas 1, 2, 3, 4 and 6 in fig. 7), may be viewed as a cortical segmentation rooted in functional differentiation.

Another result of the present experiment, the complete absence of degenerated thalamo-cortical fibers passing through the corpus callosum to the opposite hemisphere speaks clearly in favor of strictly unilateral connections and functional relations between the thalamus and cortex (see identical finding in Experiments II, III, and V-A). This finding is the more valuable since the lesion in this experiment involves no callosal fibers of the middle portion of the brain.

EXPERIMENT II

In this experiment, the instrument was introduced at a spot marked by the small dotted area in figure 2, in the ventral portion of the frontal lobe close to the arcuate sulcus and ventral to the sulcus frontalis principalis. The spot was chosen to avoid injury to the occipito-parietal lobe. The lesion (*L* in corresponding figures), a narrow channel scarcely more than half a millimeter wide, penetrates obliquely inward and caudalward through the most oral extremity of both the extreme and external capsules, through the rostral portion

of the claustrum (figs. 44, 45), and beyond through the ventral portion of the putamen and globus pallidus (figs. 46-49). Grazing in its course the central portion of optic tract near the external geniculate body (figs. 49, 50) and also the internal (medial) segment of the

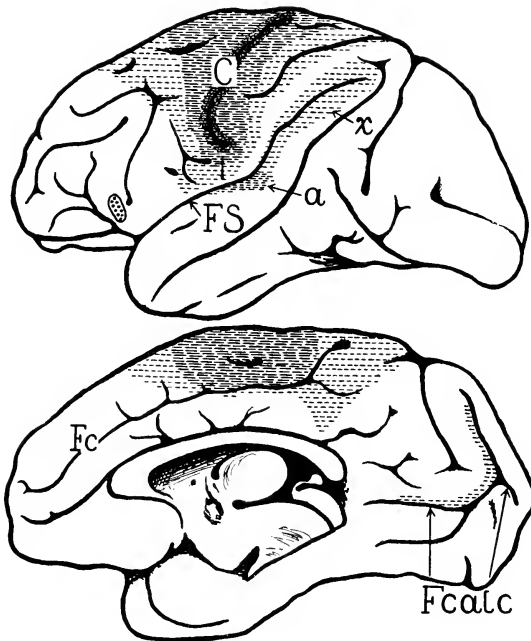


Fig. 2, Experiment II. External (upper figure) and internal (lower figure) face of the monkey's hemisphere showing the location and extent of the three projection regions of the cerebral cortex found in this experiment (shaded areas). Somatic sensory region on both sides of the central sulcus (*C*) and above the fornciate sulcus (*Fc*); auditory region, small deeply shaded area (*a*) below the Sylvian sulcus (*FS*) and a projection region of unknown significance along the posterior portion of the Sylvian sulcus, lightly shaded area (*x*); visual area in the upper lip of the horizontal branch of the calcarine fissure (*Fcalc*) and in front of the ascending branch of that fissure. Differently shaded areas indicate difference in number of afferent fibers. Small dotted area in the frontal lobe represents the superficial lesion through which the knife was introduced into the substance of the hemisphere. (Compare figs 44-62 and 65.)

latter (fig. 51), it finally enters the internal capsule and the dien-cephalon (figs. 48-51). Within the internal capsule, the lesion simulates almost exactly the shape of this region, reaching upwards as far as the tail of the caudate nucleus, without, however, damaging the

latter. In fact, the lesion misses the rostral portion of the anterior limb of the internal capsule, destroying only its middle and caudal segments. Moreover, the capsular lesion enters the ventral thalamic and subthalamic regions (figs. 50-52). Within the diencephalon, a greater part of the zona incerta and of the thalamic or subthalamic region in front of it, escaped the injury. Thus both fields of Forel, the stratum intermedium of the peduncle and the corpus subthalamicum of Luys remained almost entirely outside the injury. Part of the injury follows the ventral portion of the external medullary lamina passing through the ventro-lateral nucleus of the thalamus as far medialward as the lateral boundary of the areuate nucleus of Forel and approaches the nucleus of Luys. Other thalamic nuclei were not directly injured. Since the capsular lesion, however, occupies the entire posterior limb of the capsule, hence separating a preponderance of the thalamus from the hemisphere, it must be assumed that a greater part of the thalamo-cortical radiation was interrupted regardless of the amount of the thalamic injury. The thalamo-cortical constituents which possibly escaped injury are those fibers originating in the most caudal portion of the lateral nucleus, including the pulvinar (figs. 52, 53), and above all, those arising from the extreme rostral segment of the lateral nucleus (fig. 47).

The number of thalamo-cortical fibers interrupted in this experiment exceeds considerably that of Experiment I due to the extent of the lesion and to its location where all thalamo-cortical fibers converge to form a compact fiber system (for explanation see Experiment I). For this reason, the present experiment offers less opportunity for studying the origin, course, and termination of constituent divisions of the radiation. On the other hand, the completeness of its degeneration demonstrates excellently that entire fiber system.

The first feature to be discerned is the trend of by far the larger number of all thalamo-cortical fibers toward the dorsal and dorso-lateral regions of the cerebral cortex, corresponding to the convexity of the hemisphere, the remainder turning medially, toward the interhemispheric cortex and laterally, toward the opercula. The fibers leading dorsalward are of a somewhat larger caliber. The coarsest are those tending toward the convexity of the dorsal segment of both central convolutions and toward the cortex coating the upper extremity of the sulcus centralis, while those intended for the interhemispheric cortex around the cingular sulcus, as well as those for the precentral and postcentral opercula, are perceptibly thinner. Fine fibers are

especially characteristic of the cingulum. The caliber of the somato-sensory fibers of the post- and precentral convolutions respectively, differs only slightly, being in the latter a trifle less coarse. The inter-hemispheric cortex reached by the afferent somato-sensory fibers corresponds to the paracentral lobule and the praecuneus of the human brain.

In the present experiment, as also in Experiments I, III, and V-A, no thalamo-cortical fibers whatever are seen to enter the corpus callosum in order to invade the opposite hemisphere. Special emphasis is laid upon this observation because of the almost complete degeneration of the thalamo-cortical radiation and because, in the present experiment, the capsular lesion approaches the dorsal corner of the thalamus. The lesion thus transects all thalamo-cortical fibers emerging from the dorso-lateral nucleus, fibers which some investigators have claimed course toward the opposite hemisphere. Upon the present observations as a basis, as well as on Experiments I, III, and V-A, sufficient justification exists for definitely dissenting from the asserted existence of thalamo-cortical fibers decussating to the opposite hemisphere.

The bulk of thalamo-cortical fibers (*sr* in corresponding figures) undoubtedly reaches both the anterior and posterior central convolutions, especially the entire cortex lining the sulcus centralis (figs. 45-53). Caudally and orally from that sulcus the number of fibers quite gradually decreases. How far in both directions these regions extend and what parts of the cortex, especially those concealed within the various furrows, receive thalamic fibers, can be easily seen from the accompanying illustrations. The illustrations show also the approximate numerical distribution of fibers (compare Chapter VI), and indicate in the corresponding figures the cortical termination of all the degenerated fibers found.

Within the white substance of the hemisphere, the thalamic fibers exhibit great variety in their course. In the main, they do not adopt the shortest path to their respective cortical destinations. A division of the most direct fibers is represented by bundles arising from the dorsal portion of the dorso-lateral nucleus. That part of the thalamo-cortical radiation remains necessarily most distant from the convex face of the hemisphere, a frequent seat of pathological processes. (Compare identical observation in the foregoing experiment.) Yet, even these medial (internal) fiber groups show one or two slight curvatures when passing beneath the sulci. Sometimes, however, such curves are sharp and rather sudden, for example, in the more laterally

situated bundles. Where thalamo-cortical fibers form dense bundles or systems, especially if their course is an oblique one ascending ventro-dorsally and longitudinally, they might in normal preparations be mistaken for short or even for long association bundles connecting the frontal and occipital regions (figs. 50-53).

The present experiment, compared with the foregoing one, exhibits in a lesser degree, but none the less, the same arrangement of individual bundles comprising thalamo-cortical radiation, indicating a functional segregation. The most dorsal fibers, arising from the dorso-lateral thalamic nucleus directed toward the dorsal segments of both central convolutions maintain an internal position. Others, originating in the ventro-lateral nucleus, and perhaps also, from the hypothalamus, hold a lateral course along and through the putamen and along the claustrum (fig. 51); their destination is the opercular (ventral) segments of both central convolutions. Concerning these ventro-lateral bundles, the statement made regarding the medial (internal) bundles of the radiation can be repeated. The ventro-lateral bundles, also, remain well removed from the convex aspect of the hemisphere and have a good chance to escape destruction by a pathological process provided the latter does not directly involve the opercular cortex or the Sylvian fossa. In the extreme caudal and most oral sections of the present series, many short sectors of fibers are seen, indicating an oblique ascending course in both oral and caudal longitudinal directions (respectively).

An exact comparison of the thalamic fibers entering the precentral and postcentral convolutions, respectively, is not easily made. Yet, superficial examination is alone sufficient to establish the conviction that the number of afferent fibers attaining the precentral gyrus is scarcely below that reaching the postcentral gyrus. Since, however, the floor of the sulcus centralis and the adjacent narrow strip of precentral gyrus coating the anterior wall of the sulcus belong structurally to the postcentral region (compare Chapters VI and VII), a part of the dense bundles terminating in the floor of the sulcus centralis, *C* in figures 46-48, reaches a cortical area which is a part of the postcentral region. But, even so, there can be no doubt that, numerically, many thalamo-cortical fibers definitely reach the precentral region (figs. 44-46). Their number per square unit appears to be somewhat below that of the postcentral region, forming looser bundles than those in the postcentral convolution. (In fig. 45, degeneration of a thin bundle of cortico-fugal fibers was produced by a small

cortical injury of the anterior portion of the frontal opercular region; in fig. 44, another thick bundle consisting of many fine callosal and very fine cortico-caudate fibers degenerated, due to the injury *L* of the frontal cortex.)

That not only areas immediately neighboring the sulcus centralis, that is, Brodmann's areas 1, 2, 3 and 4, receive afferent fibers, but also the parietal region (in the narrow sense of that word, areas 5 and 7 of Brodmann), and the precentral area 6 of Brodmann is well demonstrated by the accompanying illustrations (figs. 52-55, and 44, 45). A small number of degenerated fibers partly composing the cingulum, as said before, also enter the cortex of the cingular sulcus. The inferior parietal or the supramarginal convolution receives only in its anterior half a somewhat larger number of thalamo-cortical fibers, more so around the intraparietal (postcentral) sulcus, although at the latter spot much less than in both central convolutions (figs. 49, 50). Caudalward, the number of afferent somato-sensory fibers in both the inferior and superior parietal convolutions noticeably decreases and finally they disappear entirely. A similar gradual decrease in number and the final disappearance of afferent fibers can be seen also toward the arcuate sulcus of the frontal lobe.

The relation between the ventral thalamo-cortical fibers and the acoustic radiation is the same as in Experiment I (fig. 51). The only exception in the present experiment is a greater number of degenerated fibers penetrating through the caudal portions of the putamen into the external capsule. In fact, all the bundles by which several small islets of the caudal putamen are separated, degenerated completely.

Ventro-lateral fiber bundles entering from the ventral thalamic region in the ventral portion of the internal capsule and forming lateral bundles of the thalamo-cortical radiation can, in quite a considerable number, be directly followed along and through the putamen and along the inner contour of the claustrum to their termination in the operculum. Yet some of them closely follow the upper spur of the claustrum and, turning laterally, penetrate into the cortex around the dorsal corner of the Sylvian fossa and lining the Sylvian sulcus (figs. 48-54). The region of the cortex which receives these afferent fibers belongs on more caudal levels to Brodmann's areas 7 and 22, that is, partly to the parietal and partly to the temporal region (*x* in figs. 52-54). In the caudal portion of the Sylvian fossa (figs. 48-51) this region forms a part of the inner dorsal wall of that fossa, maintaining its connection with the acoustic area proper (*Tr* in figs. 50, 51)

which occupies the lower wall of that fossa or the upper wall of the superior temporal convolution (T_1). Afferent fibers which enter the oral portion of that temporo-parietal receptive area (in the Sylvian fossa) are mostly thin, while those reaching the caudal portion of that area along the posterior limb of the Sylvian fissure, have, to a considerable extent, quite a coarse caliber. This new posterior Sylvian receptive field stretches along the entire posterior (occipital) extremity of the Sylvian fissure and is here separated from the proper somatosensory region by a narrow strip of cortex covering the convexity of the inferior parietal (angular) convolution (PI in figs. 52, 53). The latter receives, in this experiment, few if any afferent fibers. However, attention must be called to the fact that this posterior Sylvian region is in reality practically entirely concealed in the Sylvian fissure; the shaded area along that fissure (x in figs. 2, 10, 24) indicates only the position of that region inside of the fissure as well as its longitudinal extent. In view of the fact that beside a portion of the thalamus and of the internal capsule, also a portion of the globus pallidus and of the putamen was injured in the present experiment, it is impossible to decide whether the last described afferent fibers do actually and exclusively originate from the ventral thalamus, or whether, perhaps, they may arise elsewhere. It would hardly seem that they belong to the intrahemispheric association systems and, at least the stronger ones among them, are likely to be actual afferent fibers arising from the ventro-lateral nucleus of the thalamus and perhaps also from the metathalamus (internal geniculate body?). In that case the described posterior Sylvian region (x) would represent a portion of the common auditory projection cortex (a in figs. 2, 10), or a special receptive area of an as yet unknown functional significance (see Chapter XI, 2).

EXPERIMENT III

In this experiment only a portion of the entire thalamo-cortical radiation was interrupted within the posterior limb of the internal capsule (fig. 66). The split-like lesion (L in the figure) is located between the dorsal corner of the thalamus and the Sylvian sulcus, the level of the injury approximately corresponding with the planes of figures 33, 34 and 52 of both foregoing experiments. Interrupted by the injury, a dense bundle of ascending thalamo-cortical fibers (sr) degenerated completely, while other bundles of the thalamo-cortical radiation remained normal. The bundle which was thus caused to

degenerate, is identical with the posterior or the caudal segment or "fan" of the thalamo-cortical radiation originating in the caudal thalamic segment and supplying the caudal half of the somato-sensory cortex behind the central sulcus (shaded areas in fig. 3). Bundles of the radiation remaining normal are those springing from the oral or

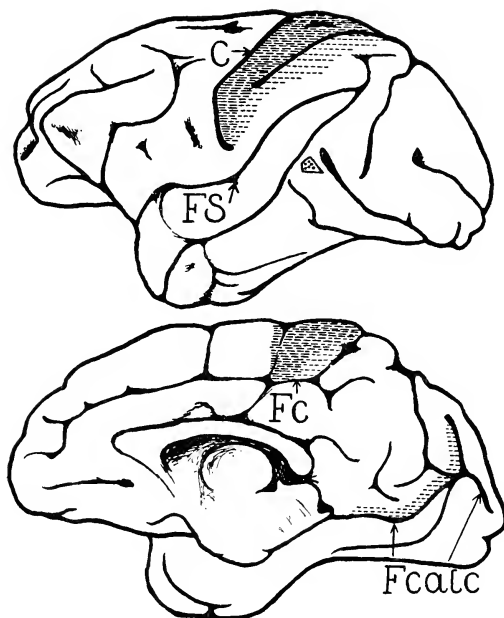


Fig. 3, Experiment III. External (upper figure) and internal (lower figure) face of the monkey's hemisphere showing the location and extent of the two projection regions of the cerebral cortex found in this experiment (shaded areas). Somatic sensory region behind the central sulcus (*C*) and above the fornicate sulcus (*Fc*); visual area in the upper lip of the horizontal branch of the calcarine fissure (*Fcalc*) and in front of the ascending branch of that fissure. Differently shaded areas indicate difference in number of afferent fibers. Small dotted area in the posterior portion of the temporal lobe represents the superficial lesion through which the knife was introduced into the substance of the hemisphere. Sylvian sulcus (*FS*). (Compare figs. 66-74.)

rostral portion of the thalamus and supplying the oral half of the somato-sensory cortex in front of the central sulcus. The degenerated portion of the thalamo-cortical radiation in great part enters the postcentral convolution and its caudal continuation which is the superior parietal convolution (figs. 66-69, 71). Only a few scattered

degenerated fibers also reach the lower parietal convolution (fig. 67). There are also a few degenerated fibers which reach the region around the most dorsal extremity of the sulcus centralis (fig. 66). From a close study of the course and cortical distribution of the degenerated fibers of the radiation it becomes evident that from the caudal segment of the thalamus fibers emanate supplying the postcentral-parietal half of the somatic sensory region, while from the rostral segment of the thalamus come those reaching the anterior half of the somato-sensory region in front of the sulcus centralis. For, that zone of the somato-sensory cortex supplied by the degenerated fibers in this experiment corresponds with the convexity of the post-central gyrus including the narrow strip of cortex covering both the anterior and posterior slopes of that convolution. The bottom of the central sulcus in contrast with the results in Experiments I, II, and V-A, receives only a few scattered degenerated fibers. The sharpness of the anterior boundary of the supplied cortical zone is remarkable; it runs below the anterior margin or lip of the postcentral convolution, in the sulcus centralis, along the entire dorso-ventral extent of that sulcus (except at its most dorsal extremity), thus leaving the anterior portion of area 3 of Brodmann which extends to the precentral gyrus, and the whole precentral region (areas 4 and 6) with normal afferent fibers.

The segmentation of the thalamo-cortical radiation into individual "fans," each arranged parallel to its neighboring fan and all fans with their planes more or less perpendicular upon the longitudinal axis of the hemisphere, which segmentation corresponds with the segmentation of the pre-postcentral cortical region into cytoarchitectural areas, appears fairly evident from this experiment. The position of the fiber fans within the internal capsule and in the white matter of the hemisphere corresponds, however, only approximately with the planes vertical to the long axis of the hemisphere. The posterior fans with their upper extremities closer to the cortex are inclined occipitalward, the oral fans oralward, thus shaping the entire thalamo-cortical radiation somewhat similar to that of an umbrella or an irregular mushroom. (Compare, especially, Experiments I, II, and V-A.) Thus the somatic sensory fibers are assembled into definite sub-systems already in the white substance of the hemisphere. The form or shape of the fiber "fan" of the thalamic radiation which degenerated in Experiment III, as well as the shape of the cortical area supplied by it, would be different if the arrangement of fibers in the subcortical white substance were another, or irregular, or a "diffuse" one. It appears

probable, therefore, that the entire thalamo-cortical radiation consists of regularly arranged fiber laminae; each of these, beginning with its thalamic origin to its cortical termination, has its own course, as well as its separate cortical terminal area. These fiber laminae do not appreciably mix with each other. The significance of such an organization of the thalamo-cortical radiation appears to lie in the preservation of the "spatial" relationships existing in the somato-sensory receptive surfaces of the body, its purpose being to isolate the conduction of somato-sensory impulses, different according to the qualities and localities, up to the definite areas or segments of areas of the somato-sensory cortex. (Compare: Visual System and Chapter XIX, in the present work.)

The present series demonstrates also the course of that portion of the thalamo-cortical radiation which ascends toward the most caudal segment of the somato-sensory region corresponding to areas 5 and 7 of Brodman (figs. 67-69, 71, compare also figs. 36, 37, 52-55). This part of the somatic sensory radiation appears as the most dorsal portion of the external sagittal layer of the parietal lobe running close to the central visual paths (*vr* in corresponding figures), especially to that part of it which finally enters into the upper lip of the calcarine fissure. (It would appear that this portion of the thalamo-cortical radiation was included by Monakow and some other investigators in their too extensive "visual radiation"; see: Visual System, in this work.)

As has been mentioned before, in Experiment III not a few descending fibers degenerated. They enter the lateral nucleus of the thalamus. The majority of these are of slight caliber, only a few being of medium size, the largest being still considerably smaller than the average thalamo-cortical fibers. These descending fibers, it is fairly safe to assume, originate in the cortex. A considerable number of them have been traced down to the roof of the midbrain, others into the cerebral peduncle. The question arises whether at least some of these fibers correspond with the cortico-thalamic fibers found by Ramón y Cajal and accepted by others (Head, Villaverde, Hollander, Wallenberg; see also Long, Mellus, Probst, Minkowski 1923-24, Riese, and my paper, 1926). All that can be said from the present study is that some of the degenerated cortico-fugal fibers which enter the ventro-lateral nucleus of the thalamus and the hypothalamus (*v.p.* of Monakow-Friedmann, ventral portion of the reticulate zone and the *zona incerta*) might indeed terminate here; this could not, of course, be settled by Marchi's method alone.

EXPERIMENT V-A

In this experiment, as in those preceding, an attempt was made to interrupt partly or totally the thalamo-cortical radiation near its origin and to study it by means of Marchi's method. With this intent a small hook-shaped lancet used in ophthalmology was thrust in a young Java monkey, through the lower part of the left angular convolution (or, what means the same, through the most posterior part of the second temporal convolution), immediately in front of the collateral sulcus. (Small coarsely stippled area in fig. 4.)

Fourteen days later the animal was killed. The lesion, as the macroscopic and microscopic examination of the left hemisphere shows, consists of a small superficial damage (1-2 millimeters in diameter) exactly between the collateral and the superior temporal sulcus. The rest of the brain appears absolutely normal. From the superficial lesion a channel begins which is directed orally and somewhat medially as it penetrates the superior temporal convolution and the dorsal half of the putamen until it reaches the internal capsule between the putamen laterally and the thalamus and the caudate nucleus medially. (Compare *L* in fig. 5.) (On the lesion in the same case causing a partial interruption of the visual radiation see Visual System, Chapter XIV, Experiment V-A.) In this way the auditory radiation passing through the ventro-caudal portion of the putamen almost completely escaped injury. (*4* in fig. 5 corresponds with figs. 29 and 49.) The damaged portion of the internal capsule corresponds with its middle third, forming the "knee" of the capsule, while its anterior and posterior portions remain undamaged. Especially the most anterior portion of the capsule, bordering on the anterior pole of the thalamus, remains outside the injury (*1* in fig. 5). The lesion of the internal capsule represents a single well delimited focus; the ascending fibers of the capsule interrupted by the lesion also represent one single sheet or "fan" of the thalamo-cortical radiation. In addition to this there is a narrow horizontal injury to the pulvinar of the thalamus, which is connected with the second injury causing the damage to the visual radiation.

The degenerated fibers of the thalamo-cortical radiation ascend from the internal capsule at the beginning as compact bundles, becoming somewhat loose within the centrum semiovale, and farther toward the central furrow, forming, on the whole, a well defined fiber system.

Fibers destined for the most dorsal segment of the sulcus centralis and for its vicinity corresponding with the centers for the lower limbs and for the anosaeral region have an almost direct ascending course (4 in fig. 5); those for the subsequent lower segments of the central

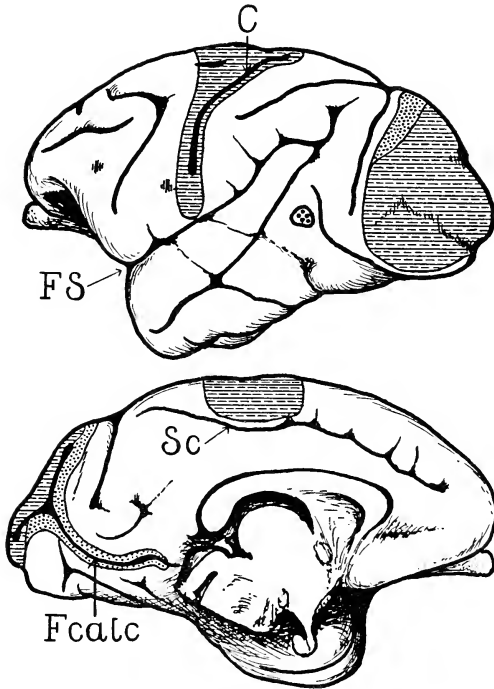


Fig. 4, Experiment V-A. External (upper figure) and internal (lower figure) face of the monkey's hemisphere showing the location, the extent, and the shape of the two projection regions of the cerebral cortex found in this experiment (shaded areas). Somatic sensory region on both sides of the central sulcus (*C*) and above the cingular sulcus (*Sc*); visual area (area striata) over the occipital lobe (upper figure), and along the calcarine fissure (*Fcalc* in the lower figure). The portion of the visual area shaded with continuous and broken horizontal lines represents the macular cortex where degenerated afferent fibers enter, in present experiment; the dotted portion of the visual cortex over the occipital lobe and over the inner face of the hemisphere along the calcarine fissure remained with normal fibers. Small dotted area in the posterior part of the temporal lobe indicates the point of entry of the instrument.

sulcus corresponding with the centers of the thorax, of the upper limbs, of the face, and so forth, are at first slightly bent and then describe even sharp curves (3, 2, and 1 in fig. 5). The thalamo-cortical

radiation as demonstrated here forms a well defined fiber system: a fiber lamina slightly twisted as it passes through the white substance of the hemisphere, with its fibers close to the internal capsule forming a compact "handle" of the "fan," and with its cortical end spreading into an elongated "umbrella," that envelops the sulcus centralis on both its sides.

The cortical region receiving the degenerated afferent fibers in the present experiment is, first, the cortex lining the floor and both the lips of the central sulcus (*C*) along its entire dorso-ventral length, which corresponds well with field 3 and probably also field 1 of Brodmann (fig. 4, compare with fig. 7). In front of the sulcus centralis a more extensive zone receives afferent fibers corresponding well in shape and position with the agranular, gigante-pyramidal or the so-called "motor" area, field 4 of Brodmann. Further, the receptive region of the cerebral cortex in this case spreads ventrally over a part of the operculum almost to the Sylvian fissure (*FS*); over the interhemispheric cortex it just reaches the cingular sulcus (*Sc*). Altogether, the somato-sensory region as delimited in the present experiment corresponds to the combined areas 1, 3, 4, and 43 of Brodmann.

As to the meaning of the result of the present experiment—it is significant that a single bundle or fan, the intermediate one, of the thalamo-cortical radiation, interrupted within the internal capsule, terminates in a cortical zone which according to its position along the central sulcus, according to its extent in front and behind that sulcus and on the inner face of the hemisphere, and according to its wedge-like shape, corresponds almost exactly with the combined cyto-architectural areas 1, 3, 4, and probably 43 of Brodmann. Especially remarkable appear the sharp boundaries of the delimited zone with the sudden cessation of the degenerated afferent fibers streaming into the cortex, which recalls the abrupt cessation of the afferent visual fibers at the point of disappearance of the stria Gennari-Vieq d'Azyr. All this means, in connection with Experiment I, II, and III, that in the present experiment one single segment or "fan" of the thalamo-cortical radiation, the intermediate one, was interrupted accidentally, and further that this fan corresponds with a few adjoining cyto-architectural areas of the central region. It does not appear to be an unreasonable conclusion that the entire thalamo-cortical radiation is organized on a functional basis: to each cyto-architectural area or field corresponds a sheet, or lamina of fibers, with its plane approxi-

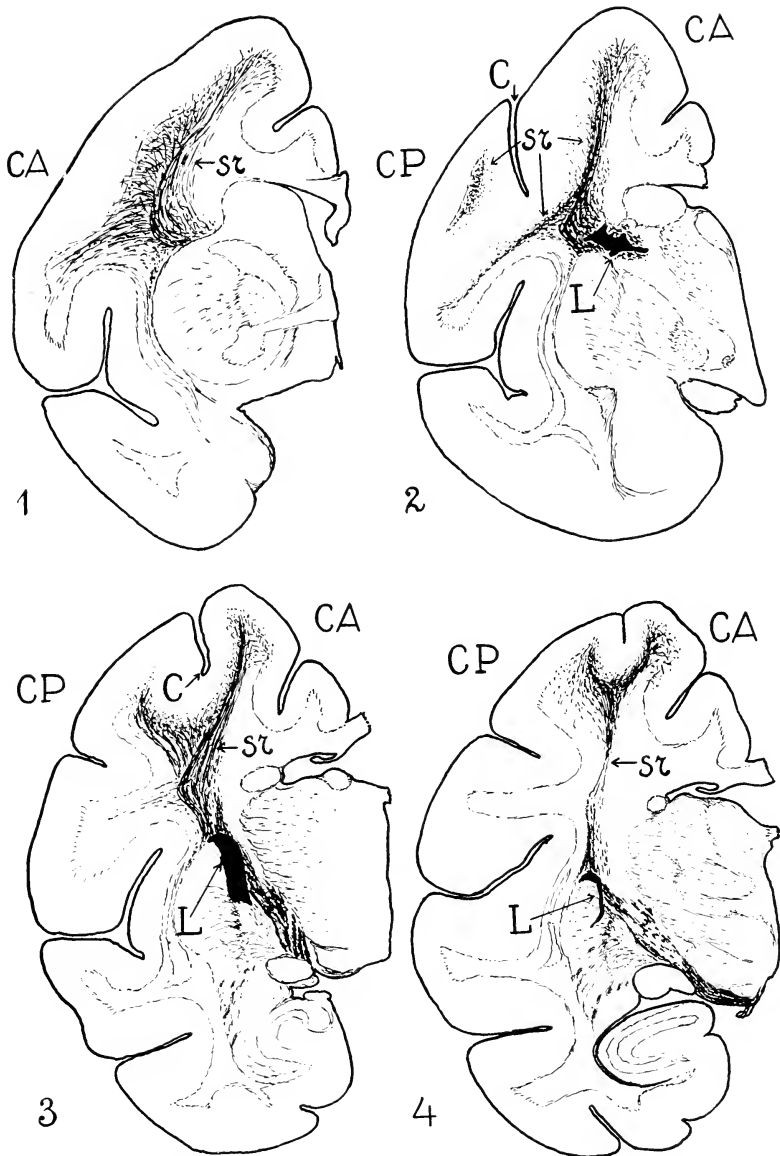


Fig. 5, Experiment V-A. This figure shows the degenerated intermediate segment or "fan" of the somato-sensory radiation (*sr*), interrupted by a single lesion (*L*) of the "knee" of the internal capsule, ascending toward the cortex covering both the precentral (*CA*), and the postcentral convolution (*CP*), and also that lining the central sulcus (*C*). (Compare with fig. 4.)

mately perpendicular to the long axis of the hemisphere and of the thalamus. This probably means a subdivision of the investigated fiber system according to certain qualities of somatic sensations. On the other hand, every one of the fiber sheets in its turn has to be imagined as being composed of individual bundles, each of which enters a segment of a particular cyto-architectural area corresponding with a special "center" according to the segmental representation of the peripheral parts of the body. In other words, just as there is a definite "spatial" arrangement in the efferent systems of the cerebral cortex, as for example in the pyramidal system where each of its bundles arise from a definite small sector of the precentral "motor" area, so there is a similar organization within the somato-sensory afferent system with this notable qualification: that there are several parallel afferent somato-sensory systems which seem to correspond with the various qualities of the sensation conducted. A somatotopic or a "spatial" organization of the afferent somato-sensory system stands parallel in organization to the visual afferent system: similar requirements of function have produced similar anatomical consequences. (Compare Chapter XIX.)

The present experiment gives additional proof that the precentral "motor" area is at the same time a receptive-sensory region.

Further it was found, as in the preceding experiments, that no afferent somato-sensory fibers enter the corpus callosum to reach the opposite hemisphere. The somato-sensory radiation is unilateral from its origin in the thalamus to its termination in the cortex.

The afferent fibers appear to be numerous everywhere in the cortex of the delimited region, possibly even more abundant in the floor of the central sulcus; and the total as well as the relative number of afferent fibers within the precentral "motor" cortex is quite considerable.

As in preceding experiments, the intracortical afferent fibers show the same characteristics and the same differences between the precentral and the postcentral regions to be described in Chapter VII. In the postcentral cortex their course is somewhat oblique, while in the precentral cortex their course is more direct and perpendicular, going for long distances in approximately the same direction.

Finally, by the lesion of the internal capsule and of the lentiform nucleus, a considerable number of efferent fibers which descend into the pes pedunculi were interrupted.

CHAPTER VI

EXTENT AND BOUNDARIES OF THE SOMATO-SENSORY
CORTEX

It should be remarked at the outset that my investigations decidedly plead for the acceptance of a far more extensive portion of the hemisphere as a somatic sensory region (fig. 6) than that accepted by most contemporary neurologists. It is secondary to the question as to what special sensory function should be attributed to each of the particular cytoarchitectural areas of this extensive region (see Chapters VIII, IX). A wide extent of the somato-sensory region on both sides of the sulcus centralis *C* is evident from Experiment I (fig. 1), from Experiment II (fig. 2) and from Experiment V-A (fig. 4), and its extent behind the central sulcus from Experiment III (fig. 3); (variously shaded areas in the accompanying figures are those receiving various numbers of thalamic fibers).

Over the external face of the hemisphere, Experiment I (fig. 1) shows a somewhat smaller extent of the somato-sensory cortex in front of the central sulcus, that cortex reaching more oralward in Experiment II (fig. 2). This is due to the fact that in Experiment II the lesion is much larger, separating a greater portion of the thalamus from the rest of the hemisphere (figs. 48-51), its oral end being also more anterior than the lesion in Experiment I (the plane of fig. 48 corresponds to that of fig. 28). This resulted in a larger portion of the anterior half of the thalamus being left normal in Experiment I than in Experiment II. Consequently a smaller part of the thalamo-cortical radiation, that is, of its rostral "fans," degenerated in the first experiment. In both Experiments I and II, the somatic sensory region determined in this way comprises on the convex face of the hemisphere the following cytoarchitectural areas of Brodmann: 1, 2, and 3, or the entire postcentral region of Brodmann, then area 5, and the oral portion of area 7 of the parietal region proper (compare also Experiment III, fig. 3, where the most dorsal portion of area 7 also belongs to the somato-sensory region). In front of the central sulcus it is area 4 of Brodmann or the area gigantopyramidalis which in both Experiments I and II, receives thalamo-cortical fibers (compare figs. 1, 2, and 3 with fig. 7).

In Experiment II the somatic sensory cortex extends, however, farther orally over a greater part of area 6 of Brodmann and includes a portion of that area buried within the arcuate sulcus. This, as is easily understood, is due to the greater extent of the injury oralward in Experiment II. In Experiment III, on the contrary, by the

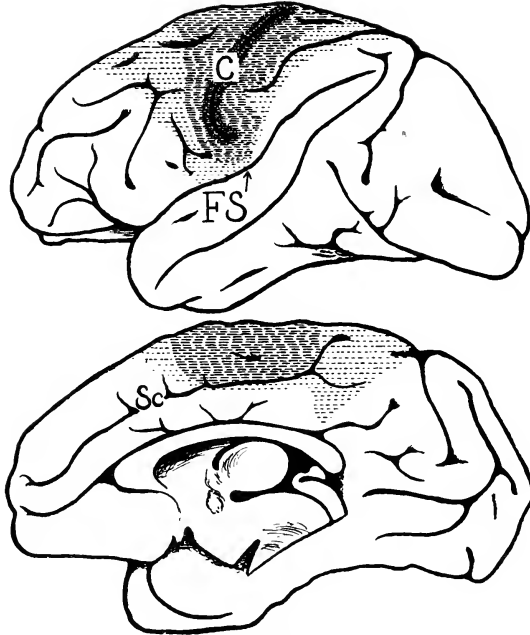


Fig. 6. A diagram showing the extension and boundaries of the "minimal" somatic sensory projection cortex in the brain of the monkey as determined in the present investigation. Upper figure represents the lateral face of the hemisphere. Here the somatic sensory region extends rather more in front of the sulcus centralis (*C*) than behind it. Differently shaded areas indicate difference in number of afferent fibers. The "nuclear or focal zone" of the entire somatic sensory region, that is, the zone receiving the greatest number of afferent fibers, is indicated by a narrow, deeply shaded area on both sides of the central sulcus. This area is in reality completely submerged in the central furrow. (Compare with figs. 9, 48, 60.) Lightly shaded areas are those receiving a correspondingly smaller number of afferent fibers. Lower figure shows the extent of the somatic sensory projection cortex on the internal face of the hemisphere. Sylvian sulcus (*FS*), cingular sulcus (*Sc*).

accidental location of the injury, only caudal segments or "fans" of the thalamo-cortical radiation destined to supply the postcentral half of the entire somatic sensory region were interrupted. Thus in all

three experiments the posterior boundaries of the presently delimited somatic sensory region are fairly congruent, the anterior boundaries being somewhat similar only in Experiments I and II: in Experiment III the anterior limit corresponds almost exactly to the sulcus centralis *C* in fig. 3). The Experiment V-A stands apart from the foregoing three experiments; its somatic sensory region occupies the intermediate cytoarchitectural areas 1, 3, 4, and 43 in and around the central sulcus (fig. 4). This can also easily be explained by the small lesion damaging just the "knee" of the internal capsule and leaving the anterior and posterior "fans" of the thalamo-cortical radiation undamaged (fig. 5).

On the internal face of the hemisphere the somatic sensory region occupies in Experiment I (fig. 1), Brodmann's areas 1, 2, 3, and a considerable portion of area 4, not quite reaching the cingular sulcus (*Fc*). In Experiment II (fig. 2), the extent of the somatic sensory region on the internal aspect of the hemisphere is the largest, occupying Brodmann's areas 1, 2, 3, 4, 5, and 7 entirely, and probably also a portion of the areas 6, 23, and 24. In Experiment III (fig. 3), the somato-sensory region occupies on the internal face of the hemisphere Brodmann's areas 1, 2, 3, and the portion of area 5 situated above the cingular sulcus (*Fc*). In this latter experiment, accordingly, the somato-sensory region on the internal face of the hemisphere corresponds fairly exactly with the cytoarchitectural postcentral and a part of the parietal region, leaving free the precentral or the oral half of the somatic sensory region corresponding to the anterior half of the paracentral lobule, and also the praecuneus, in the same way as found on the external face of the hemisphere. The reason is that mentioned before; namely, the fact that only the posterior segments or "fans" of the thalamo-cortical radiation were interrupted in Experiment III. In Experiment V-A the somatic sensory region over the inner face of the hemisphere in agreement with the size and the position of the lesion occupies the intermediate cytoarchitectural areas 1, 3, and 4, and just reaches the cingular sulcus (*Sc* in fig. 4).

Taking all four experiments together the "minimal somatic sensory region" of the macacus' hemisphere (fig. 6) embraces on the external face: Brodmann's areas 1, 2, 3, 5, and a considerable portion of area 7, all of which belong to the postcentral and parietal region (compare fig. 7). In front of the sulcus centralis, area 4 and at least the greater portion of area 6 belong to the "minimal somatic sensory region." Over the internal face of the hemisphere the "minimal somatic sensory region" occupies Brodmann's areas 1, 2, 3, 4, 5, and 7.

A narrow strip of cortex hidden in the sulcus cinguli and representing a portion of Brodmann's areas 23 and 24, also belongs to the somatic sensory region.

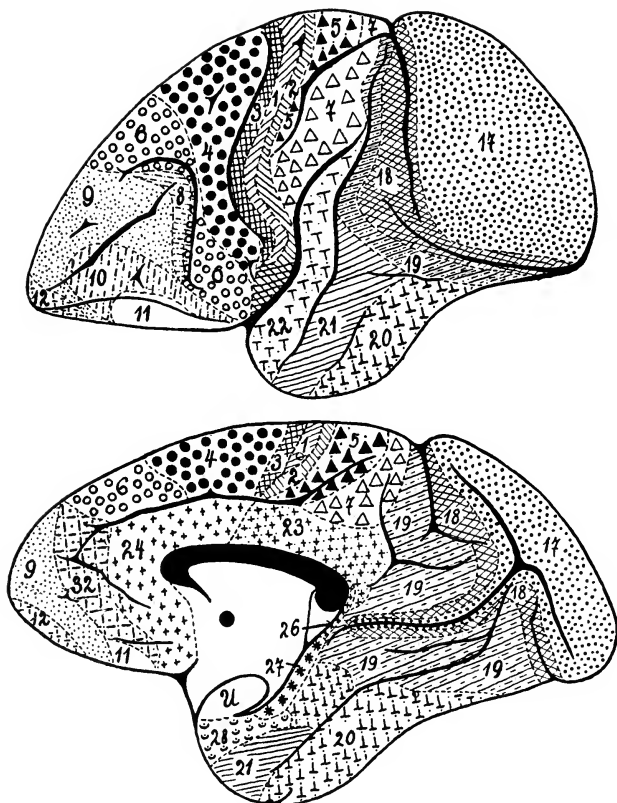


Fig. 7. Brodmann's chart of the cytoarchitectural areas and regions of the cerebral cortex in *Cercopithecus* (Brodmann, 1904-05, 1907, 1909). The area striata of Elliot Smith, Brodmann's field 17, along the horizontal branch of the calcarine fissure (lower figure), and field 3 along the central sulcus (upper figure) are in reality buried in the sulci mentioned.

The question arises as to how far the boundaries of this "minimal somatic sensory region" as determined by combining the results of all four experiments might coincide with the actual somatic sensory region of the hemisphere. To answer this attention must be called

to the following circumstances: In each of the experiments, the shape and the position of the somato-sensory area varies, considerably in front of the sulcus centralis, and somewhat less behind that furrow. This is caused by various sizes and locations of the intrahemispheric injuries, as is easily seen from a comparison of the accompanying illustrations. Yet the Experiments I, II, and III have in common the degeneration of caudal or posterior "fans" of the thalamo-cortical radiation which have been interrupted in all three experiments in almost an identical way. Moreover, in Experiments I and III the pulvinar and the posterior segment of the lateral nucleus of the thalamus were practically separated from the hemisphere. This indicates that in these experiments all or nearly all caudal "fans" of the thalamo-cortical radiation must have been caused to degenerate. For that reason it is probable that the posterior boundaries of the presently delimited somatic sensory region come near to its actual limits.

The same is also probable in respect to the extent of the somatic sensory cortex toward the cingular sulcus and toward the Sylvian fissure. In both Experiments I and II, the most dorsal as well as the most ventral bundles of the thalamo-cortical radiation were interrupted.

The oral or anterior boundary of the "minimal somatic sensory region" found here, on the contrary, probably falls short of its actual limits. That the sulcus centralis can in no way be accepted as the oral limit, which might seem plausible from Experiment III, is evident from a comparison with Experiments I, II, and V-A. In all of these experiments where the thalamic and capsular lesion reaches more frontalward, the limits of the respective sensory region also came to lie more orally. Indeed, if our experience were limited to Experiment III alone, this would probably lead to the erroneous conclusion that the somatic sensory region occupies the postcentral region only, an error actually committed by some previous investigators. It, therefore, must be regarded as fairly safe to accept the anterior boundary of the somatic sensory region found here as a "minimal" one (fig. 6). It is, however, not possible to decide whether the somatic sensory region does not, in fact, reach beyond the oral boundary determined in the present investigations, and, perhaps, embrace parts of the frontal cortex (*regio frontalis*) anterior to these limits. It is necessary to bear such a possibility in mind in view of the fact that in neither of the present experiments was the most rostral portion of the lateral nucleus of the thalamus destroyed (compare figures in front of both

figs. 28 and 48). There might only linger as regards Experiment II the possibility that the capsular lesion, indeed, interrupted all or almost all fiber "fans" arising from the rostral portion of the thalamus. Nevertheless, considering a wider extent of the frontal region receiving thalamic fibers and found to be concerned with sensation in the experiments and studies of Monakow, Flechsig, Probst, Quensel, Roussy, Sachs, Meier-Müller, Tsunesuke Fukuda, Minkowski, and Dusser de Barenne (fig. 8), we must necessarily regard the anterior

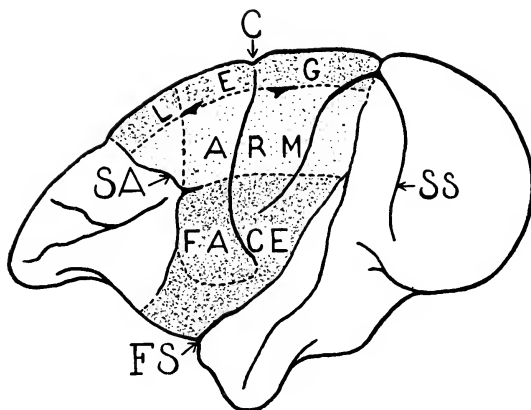


Fig. 8. Somatic sensory region in the monkey according to Dusser de Barenne (1925). It occupies an extensive region both in front and behind the central sulcus (*C*). Anteriorly it reaches the arcuate sulcus of the frontal lobe (*SA*) and extends as far back as the superior temporal and the Sylvian sulci (*FS*). Simian sulcus (*SS*).

limits of the somato-sensory region of the hemisphere as an unsettled problem until it is shown where the fibers originating from the most anterior segment of the lateral thalamic nucleus actually terminate.

In any event, even granting that the actual boundaries of the somato-sensory cortex lie farther from the central sulcus than is here indicated, it is clear from the present investigation, that the somato-sensory region of the hemisphere does not occupy merely a narrow strip of cortex posterior to the sulcus centralis as accepted by nearly all present day neurologists. It occupies in fact, a wide region including the postcentral region, a considerable portion of the parietal region, and almost the entire agranular precentral region. It surely does include the entire electrically excitable or the so-called motor

area for detailed (special) movements, area praecentralis *giganto-pyramidalis* or field 4 of Brodmann, and also field 6 of that investigator. (Compare *Economo-Koskinas*, pp. 288, 312, 538.)

I would here touch upon a few points in the work of previous investigators which are not in accord with the present results. *Sachs* (1909) in his experimental work on the thalamus observed almost all thalamo-cortical fibers to turn toward the precentral and frontal cortical regions, the reverse of my Experiment III. The lesions in his experiments, besides being too small to permit an estimate of the numerical distribution of thalamo-cortical fibers to various portions of the somato-sensory cortex, were practically all situated within the anterior or rostral half of the thalamus, leaving the pulvinar and the posterior half of the thalamus mostly unaltered. From what has already been said about the internal arrangement or the segmentation of the thalamo-cortical radiation it seems clear, that in *Sach's* experiments, preponderantly, if not exclusively, the anterior or the rostral portion of the thalamic radiation was partly caused to degenerate. In the work of other investigators (*Probst, Roussy*), where extensive lesions of the thalamus and internal capsule were produced, there was also a degeneration of both visual and auditory central paths. These latter fibers were not sufficiently discriminated from the proper thalamo-cortical radiation. By confounding both geniculo-cortical radiations with a portion of the thalamo-cortical radiation proper, these investigators erroneously claimed a greater part of the cortical surface, including the parieto-occipital lobe and a part of the temporal lobe, as the somatic sensory region. *Monakow* fell into similar error, although in his case this was more excusable, for his technique was inadequate. He proclaimed the occipito-tectal efferent fiber system which passes through the ventral pulvinar as a pulvinaro-cortical and mesencephalo-cortical afferent path. (Compare fig. 96.)

Besides the areas on both sides of the sulcus centralis and the neighboring portion of the cortex on the internal face of the hemisphere (rendering that sulcus comparable to the fissura calcarina), all of which might justly be regarded as the somatic sensory region in a broad sense (*Brodmann's* areas 1, 2, 3, 4, 5, 6, 7, and 43), there has been found in Experiment II, a special temporo-parietal (posterior Sylvian) receptive region also receiving afferent fibers (area *x* in figs. 2, 10, 24). Because of the location of the lesion in that experiment, as explained in the foregoing paragraphs, it cannot be denied that some of the fibers entering that cortical region might be associational

or those originating from the lenticular nucleus. Nevertheless, it is certain that at least the greater majority of the fibers supplying this new receptive region, and especially the large calibered ones tending toward the posterior extremity of the Sylvian fissure (fibers marked with *x* in figs. 52-54), belong to an afferent fiber system originating either in the internal geniculate body or somewhere in the ventro-lateral nucleus of the thalamus or even in the hypothalamus. (In Experiment I where the ventro-lateral nucleus was damaged to a small extent only, these fibers remained mostly normal, while in Experiment III, a few of them degenerated.) That cortical area, accordingly, also, belongs to the receptive regions of the hemisphere.

The above mentioned posterior Sylvian receptive region is almost entirely hidden within the Sylvian sulcus, appearing on the free face of the hemisphere only in the most caudal portion of the supramarginal convolution (*x* in fig. 54). This region is in reality continuous along the posterior part of the Sylvian fossa and along the entire posterior extremity of the Sylvian fissure. It occupies the lower portion of Brodmann's area 7 and the upper portion of area 22, suggesting another division of that part of the parietal and temporal regions than that made by cytoarchitectural studies. The "nucleus" of this posterior Sylvian receptive region might correspond very well with Brodmann's dorso-caudal portion of the insular region hidden in the Sylvian fossa which possesses a well formed inner granular layer (see Brodmann, 1909, p. 156), and is otherwise distinguished in the monkey's brain by an intra-cortical fiber layer not unlike the inner stripe of Baillarger. The region in question extends, however, farther caudally and does not possess sharp limits comparable to those of the striate area. Only by new detailed investigation can it be decided whether this posterior Sylvian region in the monkey is an homologue of the parietal areas covering the angular convolution in the human brain (Brodmann's area 40, and perhaps also, his areas 39 and 22; area PF and perhaps PG of Economo-Koskinas), which have a distinct function; or whether, as appears probable, this region is nothing other than the caudal or posterior extension of a much wider auditory area than is usually accepted, corresponding in the human brain to the entire granular cortex which occupies, according to the delimitation of Economo-Koskinas, the posterior Sylvian fossa, the greater part of the superior temporal convolution, the angular and the supramarginal convolution. (See also Chapter X and XI, 2.)

CHAPTER VII

CORTICAL TERMINATIONS OF SOMATO-SENSORY
AFFERENT FIBERS

In the same uninterrupted series of the brains of *Macacus* described before and stained according to Marchi's method, the minute relations of the intracortical terminations of thalamic fibers were studied. Experiment II proved to be especially valuable since the completeness of degeneration of the thalamo-cortical radiation apparently reached its maximum here. It was, therefore, assumed that the preparations of cortex where compact fiber bundles enter show, in this series, a complete picture of all the existing intracortical terminations of the afferent somato-sensory fibers. The identity of degenerated intracortical fibers in Experiments II, III, and V-A where the radiation was interrupted outside the thalamus, and that of the actual thalamo-cortical fibers was easily established by comparing them with Experiment I, where no doubt could arise as to the thalamic origin of similar fibers.

The mode of termination of thalamic fibers within the somatic sensory cortex so far, of course, as this could be determined by Marchi's method, in particular the relation of fibers to special cell and fiber layers of the cortex and other characteristic features such as the size, course, and numeric distribution of fibers to various cytoarchitectural areas given below, is a combined result drawn from all four experiments.

Thalamo-cortical fibers as said before (see Chapters V and VI) reach an extensive territory of the hemisphere. Since, as mentioned previously, afferent somato-sensory fibers are most dense around the central sulcus (narrow, deeply shaded area in fig. 6 completely submerged in the central furrow) their minute relations were most conveniently studied here.

Penetrating into the cortex of the bottom (fundus) of the central sulcus, somato-sensory fibers invade in a great number the lower third of the cortex near the subcortical white substance (figs. 9, 60 represent the dorsal extremity of the sulcus centralis showing a portion of fig. 48 at a higher magnification; in fig. 9 all details in the drawing, except the outlines, represent degenerated fibers). Here numerous

short and long segments and particles of coarse, as well as of medium sized and fine blackened degenerated fibers can be seen. Many of them have an oblique or a horizontal course running for a considerable distance in the ventral strata, others ascend in a more irregular or even in a straight way upward toward the middle cortical layers. However, hardly any degenerated fibers exist in that cortical area



Fig. 9, Experiment II. This figure represents a portion of figure 48 at a somewhat higher magnification, demonstrating the relation of the afferent thalamic fibers to the cortex of the sulcus centralis (*C*). In this experiment the somatic sensory radiation degenerated almost completely. The bulk of the afferent fibers (all details in the figure except the outlines of the cortex represent degenerated fibers) enter as dense bundles into the cortex lining the bottom of the sulcus centralis (*C*), while the number of fibers decreases toward the convexities both of the precentral (*CA*) and of the postcentral convolution (*CP*). In the cortex of the bottom of the central sulcus, afferent fibers reach the stripes of Baillarger (dotted, sickle-shaped intracortical stripe); a few fine fibers reach even the supragranular layers. This cortical area with the best afferent fiber supply and the best developed granular layer and Baillarger's stripes is the "nuclear or focal zone" of the entire somatic sensory cortical region of the hemisphere. It corresponds with field 3 of Brodmann. (Compare figs. 6, 7.)

which resemble actual "radiated bundles" (these latter are cortico-fugal as well as incoming associational—figs. 63, 64—and callosal fibers, as other experiments in the present work show). Also no "radiated fibers" remaining normal were noticed here or were at any rate not visible because of the extremely dense meshwork of degenerated fibers. These latter in a considerable number approach and finally enter the stripes of Baillarger, the latter being particularly well marked in the central sulcus (the mentioned stripes represented by the upper semi-circular layer in figs. 9 and 60 filled with black detritus). In that region the inner and the outer stripe of Baillarger as well as the layer between them seems to contain no other fiber elements except the blackened detritus of fairly coarse and fine particles of the disintegrated myelin. A few solitary and very fine, fairly long degenerated fibers of a more straight and also of an irregular oblique course, penetrate even into the upper cortical strata above the external stripe of Baillarger. In our figure 60, the upper semicircular layer corresponds with the lamina interstriata and probably with both the inner and the outer stripe of Baillarger according to Vogt's (1919) terminology. (Compare his figs. 19, 29, and 69.) The peculiarities of the intracortical somatic sensory fibers which have just been described, namely: (a) their frequently oblique ascending or horizontal course in the lower strata, (b) their considerable size, (c) the well developed inner and outer stripe of Baillarger containing numberless medium sized and fine degenerated fibers, and (d) the presence of a few degenerated fibers of a fine caliber in the upper strata above the stripes of Baillarger—are all present in both walls of the sulcus centralis, hardly more in the posterior than in the anterior; yet of the cortex of the actual bottom of the central sulcus and of the adjacent cortex they are best expressed in the bottom (figs. 9, 47-49, 60). The posterior wall of the central sulcus shows toward the convexity of the postcentral convolution a slight gradual decrease of the number of the intracortical somato-sensory fibers, the stripe of Baillarger also loses its distinctness in that direction (fig. 9). The anterior wall of the central sulcus belonging to the precentral convolution shows also a similar although hardly a more rapid decrease of the number of the intracortical terminal afferent fibers. At no point, however, was there noticed an abrupt cessation or disappearance of the rich intracortical exogenous meshwork or of the Baillarger's stripes. It is also noteworthy that in the cortex of the fundus of the central sulcus, in contradistinction to the convexities of both the pre- and post-

central convolutions, degenerated fibers of a more or less straight radiated character are entirely absent (though in the convexities too they, for the most part, do not exactly correspond with the actual "radiated bundles," figs. 58, 59, 61, 62). It also ought to be mentioned once more that the number of cortico-petal fibers in the bottom of the sulcus centralis exceeds the number of intracortical afferent fibers of the acoustic "focal zone" in the superior temporal convolution (recte in the upper wall of that convolution hidden in the Sylvian fossa), and appears even somewhat larger than the number of the visual afferent fibers in the striate area found in the present experiments, which coincides with Vogt's observations. (This might be partly attributable to the larger caliber of the somato-sensory fibers; compare fig. 60 with fig. 65; see also Visual System.) The described narrow strip of the somato-sensory cortex along the bottom of the sulcus centralis corresponds well with area 3 of Brodmann.

An essentially similar relationship between the intracortical terminations of the thalamic fibers and cortical structures, although with some differences, was found in the cortex of the convexity of the post-central convolution corresponding with areas 1 and 2 of Brodmann. (Compare figs. 58, 59 which correspond with the posterior lip of the central sulcus in figs. 9, 48.) Here the number of exogenous intracortical, moderately coarse, and coarse thalamic fibers (black lines and dots in the corresponding figures), is already considerably smaller than in the cortex of the bottom of the sulcus centralis. Also a few of them take a course more or less similar to that of the "radiated bundles," the latter remaining otherwise perfectly normal (yellow lines in accompanying figures). The majority of the somato-sensory terminal fibers here too, however, have an oblique ascending course toward the middle strata quite distinct from the actual "radiated bundles." Numerous intracortical fibers, and not only those near the white subcortical substance, but also those close beneath the inner stripe of Baillarger take a more or less horizontal course. These fibers which often traverse long distances, can be seen especially in sections whose planes lie parallel to the long axis of the postcentral convolution. They resemble similar subcortical afferent somato-sensory fibers immediately beneath the cortex. In areas described here, fewer degenerated somato-sensory fibers reach the inner stripe of Baillarger, from where they often proceed for a short distance in a horizontal direction. (Compare Ramón y Cajal, 1909-11. vol. 2, p. 641, fig. 406, with my figs. 58, 59; in my figures the inner stripe of Baillarger is seen in the upper

portion of the figures.) Some of the finer fibers were seen traversing long stretches in the lower strata along the inner contour of the cortex; yet the same kind of fibers was also observed in a few instances in the inner stripe of Baillarger itself. In the precentral and the postcentral cortex corresponding with the convexities of both central convolutions, in contradistinction to the bottom of the central sulcus, no degenerated fibers were found in the upper strata above the outer stripe of Baillarger.

A little further back caudally on the convexity of the postcentral convolution close to the intraparietal or postcentral sulcus corresponding approximately with Brodmann's area 2, there exist hardly any appreciable differences as to the number, course, and so forth of the intracortical somato-sensory fibers when compared with the oral half of the convexity of the same convolution corresponding with area 1 of Brodmann. Yet a decrease of the exogenous intracortical fibers is noticeable in that portion of the somato-sensory cortex which coats the postcentral sulcus, and on the inner face of the hemisphere.

In the precentral convolution, that is, in Brodmann's areas 4 and 6 the behavior of the afferent somato-sensory fibers is less complicated especially when compared with the inextricable meshwork around the bottom of the sulcus centralis, as described above. (Compare figs. 61, 62, with figs. 58-60.) While particularly in the latter area the degenerated afferent fibers form a dense plexus of more or less irregularly arranged fibers (figs. 9, 60), their courses in the subcortical white matter and within the voluminous precentral cortex are straighter, being for comparatively long distances in the same direction (figs. 61, 62). Accordingly, there are only a few more or less "horizontal" fibers below the precentral cortex and in that cortex itself, at any rate, less than found in the postcentral cortex. Although the majority of the afferent somato-sensory fibers of the precentral cortex approach more the course of the "radiated bundles," they, too, must mostly be kept apart from the actual "radiated fibers." They for the most part cross the "radiated bundles" at a sharp angle. As to the number of the somato-sensory fibers in the precentral cortex, this is hardly below that found in the cortex covering the convexity of the postcentral convolution. Considering, however, the wider extent of the precentral region, the total number of the afferent intracortical fibers probably exceeds such fibers entering the postcentral-parietal areas, with the exclusion of area 3 of Brodmann.

In general it can be said that the number of the intracortical terminal somatic sensory fibers gradually decreases from the bottom of the central sulcus, where it is the greatest, towards the limits of both the precentral-frontal half as well as of the postcentral-parietal half of the common somato-sensory region. (Compare *CA* in figs. 26, 27 with *CP* and *PS* in figs. 29, 30, 34, 36, 37 of Experiment I; F_1 and *CA* in figs. 44, 45 with *CP* and *PS* in figs. 50-53 of Experiment II; and *PS* in figs. 66-69 of Experiment III.) The same gradual decrease was observed toward the Sylvian fissure and toward the cingular sulcus (for example figs. 46-49). Near the boundaries of the common somato-sensory region of the hemisphere, the widest extent of which is demonstrated in Experiment II (fig. 2), the number of the intracortical sensory fibers becomes gradually so very much reduced as to be represented by a few scattered, fine, or medium sized fibers to be found now and then. Thus various cortical areas of the common somato-sensory region show wide differences in respect to the wealth of the afferent fibers. An attempt has been made to demonstrate this by differential shading of the areas in the accompanying illustrations (figs. 1, 2, 3, 6, 24). The diagrams, however, do not fully portray the actual conditions for they do not show adequately the gradual decrease of fibers. Differential shading is intended only to show the approximate abundance of fibers of the several zones: (a) of the richly supplied areas in the sulcus centralis and in its neighborhood, corresponding with Brodmann's areas 1, 2, 3, and 4, which contain from very numerous fibers (area 3, the narrow deeply shaded area on both sides of the sulcus centralis in the accompanying figures in reality buried in the sulcus itself) to fairly numerous ones (double shaded areas on both sides of the sulcus centralis in these figures corresponding with areas 1, 2, and 4 of Brodmann), while (b) the remaining parietal and frontal areas (lightly shaded areas in the accompanying figures), corresponding with Brodmann's areas 5, 7, and 6, which form a peripheral belt or zone of the common somato-sensory region, contain from rare, loose fiber bundles to a few scattered individual fibers. Although the transition from one area to its contiguous neighbor, as has been said, is a fairly gradual one, the limits of differently shaded areas as given in the accompanying diagrams based on repeated minute examination of the three continuous series, do roughly indicate the richly and poorly supplied areas. On the other hand, it is fairly certain that the remaining regions of the hemisphere left outside the shaded areas in figures 1, 2, 3, and 4, are

those where no degenerated afferent somato-sensory fibers whatever were found in the present experiments.

The absolute number of the afferent fibers of the entire somatic sensory region of the hemisphere must be estimated as quite considerable, exceeding that of the visual fibers of the striate area and being considerably above that of the auditory projection cortex. (This, it must be admitted, might only appear to be so since the somato-sensory fibers have, on the whole, a stronger caliber than the visual, producing a more intensive degeneration.) The relative number of the intracortical afferent fibers of the precentral half of the somatic sensory region (areas 4 and 6) if compared with the postcentral-parietal half of the same region (areas 1, 2, 3, 5, and 7) is likely to be equal, although the fibers are more condensed in the narrow post-central strip of cortex around the bottom of the central sulcus, that is, in area 3.

Thus, according to the results obtained in the present experiments, there exists a wide region of the hemisphere which receives fibers of thalamic origin and extends about equally, orally and caudally, from the sulcus centralis as well as over the internal face of the hemisphere where it reaches the sulcus cinguli. Most richly supplied with the thalamo-cortical fibers is a narrow zone corresponding with the entire length of the sulcus centralis from the dorsal margin of the hemisphere down to the Sylvian fissure. This zone is entirely buried within the central sulcus, occupying both walls of that sulcus, although partly only. Accordingly, this zone around the bottom of the sulcus centralis must be regarded as the "nuclear or focal zone" of the entire somatic sensory region. Whether this zone belongs partly only, or, perhaps entirely to the postcentral granular region, has not been possible to decide conclusively, by studying the Marchi's series alone, although considering the facts obtained by students of the cortical cytoarchitecture and myeloarchitecture in primates and in man (Brodmann, Vogt, Mauss, Nañagas, Economo-Koskinas) one would be inclined to believe that it corresponds wholly to the granular postcentral region, and is identical with its most anterior portion where the inner granular layer is best developed (area 3 of Brodmann in the monkey and in man, areas PA and PB of Economo). This also stands in good accord with Vogt's finding the number of very coarse oblique and horizontal fibers in lower cortical layers to be greatest in the posterior lip of the central sulcus (Vogt's areas 67 and 69; see also Roussy, Mauss, and Flechsig, 1920). A second zone, less well supplied than the first

though still containing numerous thalamic fibers, occupies the greater part of the convexities of both the postcentral and the precentral convolutions and the nearby portions of both lips of the central sulcus which do not belong to the "focal zone." A third zone occupying the "periphery" of the common somatic sensory region of the hemisphere, belonging partly to the frontal lobe and partly to the parietal lobe, receives only a small number of scattered thalamo-cortical fibers. But, as was said above, the transition from one zone to its neighbor is a fairly gradual one.

As to the numerical distribution of somato-sensory afferent fibers to various portions or segments of both the precentral and postcentral convolutions corresponding with the individual "centres" for detailed or special motor acts in the precentral cortex, or to definite representations of a conscious sensory function, that is, to the so-called sensory "centres" of the postcentral region, there has been found scarcely any appreciable difference. If there are any differences, the intermediate segments of the postcentral region between the anterior extremity of the postcentral-parietal sulcus and the sulcus centralis receive a little more numerous thalamo-cortical fibers, while the most ventral (opercular) segments of the same region are perhaps a little less abundantly supplied, which also can be noticed in the accompanying illustrations. The first mentioned segments would correspond to the somato-sensory representation of the hand and of the fingers in the monkey's brain (Vogt, 1919, fig. 125) and very probably also in the human brain (Foerster, 1927); the opercular region would represent the tongue, the face, the neck in the monkey (Vogt), and, as might be added, probably also the entire inner surface of the mouth, nose, and throat (Foerster). Surely in no one of my experiments is the afferent somato-sensory fiber supply of the opercular segments of both central convolutions as abundant as might be expected; and, as a matter of fact, the somatic sensory region of the hemisphere as delimited here barely reaches the Sylvian fissure. (This result might be the consequence of the location of the lesion; here, of course, Experiments I, II, and V-A must be considered more than Experiment III.) Of the most dorsal segment of the postcentral-parietal convolution (that is, of the superior parietal gyrus), it is only the convexity which receives a considerable number of thalamic fibers; whereas, the posterior slope of that convolution hidden in the parietal sulcus, and the cortex covering the inner face of the hemisphere, corresponding with the caudal portion of the paracentral lobule and with

the praecuneus in the human brain, is entered by a small number of scattered afferent fibers which, however, reach the posterior extremity of the cingular sulcus (partly by way of the cingulum).

It is also noteworthy that, at least in so far as the "focal zone" of the somato-sensory region is concerned, the supply of the cortex with thalamic fibers is continuous. There are no visible gaps or small regions without afferent fibers which would alternate with cortical islets receiving such fibers, as supposed by some investigators. (Compare similar observations on the supply of the visual cortex: Visual System, in the present work.)

It can also be noticed that the shape of the areas, showing in the present experiments a richer or a poorer supply of thalamic fibers, closely resembles the shape of the cytoarchitectural areas. Thus in Experiment II (fig. 2), the area in front of the central sulcus abundantly supplied with somato-sensory fibers, has the form of a narrow triangle stretching more or less parallel along the central sulcus with a sharp point turned toward the Sylvian fissure. That area resembles closely Brodmann's area praecentralis gigantopyramidalis or the so-called motor area (area 4 in fig. 7). In front of it lies the area receiving rare thalamic fibers and corresponding, on the whole, with the precentral agranular area 6 of Brodmann, although, however, it is somewhat smaller. Caudad to the central sulcus the well supplied area in Experiment II corresponds almost exactly to Brodmann's postcentral granular areas 1, 2, and 3 embracing, however, all three mentioned areas (the postcentral region of Brodmann) where area 3 stands apart, as said before. This correspondence applies also to the medial face of the hemisphere. Less abundantly supplied caudal areas in Experiment II, however, do not completely cover Brodmann's parietal areas 5 and 7. In Experiment I (fig. 1) areas in front of the central sulcus are smaller and only both of these taken together would correspond with Brodmann's area containing giant cells, while caudad to the central sulcus the abundantly supplied area in that experiment might well correspond with Brodmann's areas 1, 2, and 3 taken together, and the less well supplied area with Brodmann's areas 5 and 7 (partly). In Experiment III (fig. 3), the region receiving afferent somato-sensory fibers is, in so far as it receives numerous fibers, a little larger than the postcentral region of Brodmann. The less well supplied region in this experiment corresponds with the anterior portions of Brodmann's parietal areas 5 and 7. (Compare also Experiment V-A, fig. 4.)

The posterior Sylvian area along the Sylvian fissure (area *x* in figs. 2, 10, 24) as found in Experiment II, is completely at odds with the usual delimitation of students of cytoarchitecture in regard to these regions, for it embraces the ventral part of the parietal area 7 and the dorsal portion of the temporal area 22. Yet even this new receptive area which is probably in close relation to the auditory function has approximately the same position as both of Brodmann's areas mentioned above that stretch alongside the Sylvian fissure.

The striking similarity between the shapes of the somato-sensory areas found here and the areas delimited by the students of cortical cytoarchitecture can be explained by the view that the structural features, that is, the cytoarchitectural and myeloarchitectural peculiarities, and to some extent also the myelogenetical characteristics of special cortical territories are the consequence of one and the same cause. They are both the manifestations of the functional specialization of each of these areas, which goes hand in hand with the structural changes. These morphological areal modifications of the originally common sensory-motor cortex are, one should assume, the expression of the increase in one area or the reduction in another, or a modification of the previously existing fiber connections, and of the creation of new connections. It is, therefore, apparent, that besides minute cyto- and myeloarchitectural arrangements, fiber connections can also be used, although perhaps with somewhat less exactness, for the delimitation of cortical areas. At least they can be used to verify the areal delimitation found by other methods and thus to corroborate or change the acceptance of certain areas or regions having the significance of functional units. Above all, the value of fiber anatomy as contrasted with that of other morphological methods of investigation lies in the fact that it is better qualified to explain the connections of definite cortical areas and consequently their functions, enabling a decision to be made as to whether certain areas must be regarded as receptive or effector centers, or perhaps as intrusted with both these functions.

It has been already mentioned that neither the boundaries of the common somato-sensory region nor those of individual areas are quite sharp, with perhaps the only exception of area 3. On the whole, the sharpness of the boundaries of the common somato-sensory cortex is not comparable with the sharp limits of the striate area, determined by cyto- and myeloarchitectural investigations and found in the present work to be identical with the boundary of the visual projection cortex. (See: Visual System.) Because of its lack of sharp delimita-

tion, the somato-sensory region reveals in general a close kinship to the auditory projection cortex. (See: Auditory System, in the present work.)

The caliber of the intracortical somato-sensory fibers exceeds somewhat that of the fibers constituting the visual radiation (see: Visual System, in the present work), and is about equal or slightly superior to that of the auditory radiation (see: Auditory System, in the present work). Yet even the coarsest among the thalamo-cortical fibers, those entering the postcentral convolution, do not quite attain the size of the strongest efferent fibers of the precentral region, the so-called pyramidal fibers. There are also some regional differences in respect to the size of fibers, since, in general, the thalamic fibers which tend toward the operculum of the precentral and parietal regions are less coarse than the rest, especially less than those entering the postcentral convolution. It also appears that quite coarse afferent fibers found in the postcentral convolutions are absent in the precentral gyrus. Somato-sensory fibers forming a close bundle or system destined for a certain cortical region, for a segment of a convolution, have approximately the same caliber; this is well exemplified, for instance, by fibers in Experiment III which reach the dorso-caudal portion of the postcentral-parietal convolution. Taking the thalamo-cortical radiation as a whole, there is an appreciable variation in the size of fibers according to different localities.

CHAPTER VIII

FUNCTION AND DISTURBANCES OF THE SOMATO-SENSORY
RADIATION AND OF THE SOMATO-SENSORY
PROJECTION CORTEX

From the above findings there can be no doubt that the somato-sensory cortex, or properly, the cortical representation of the thalamus occupies a considerably larger region than a narrow strip immediately behind the sulcus centralis. The present experiments show that the agranular precentral cortex (areas 4 and 6 of Brodmann) as well as the postcentral and parietal granular cortex (areas 1, 2, 3, 5, 43 and a part of area 7 of Brodmann) receive direct impulses from the thalamus, each region by way of its own portion of the thalamo-cortical radiation (besides those impulses which reach the precentral cortex from the postcentral by way of strong, short U-shaped association fibers, and vice versa, and other impulses from the opposite hemisphere by way of the callosal fibers, as other of my experiments show). For that reason the precentral cortex, that is, both areas 4 and 6 of Brodmann, cannot be regarded as a mere executor for the influences arriving here from the surrounding areas, notably from the postcentral cortex; for, as the disclosed connections of the precentral cortex indicate, that cortex, besides receiving impulses from the postcentral and other regions and besides the motor performances, has an afferent or receptor function of its own. In that sense the precentral region must certainly be regarded as a true sensory-motor cortex. The present view of a complete or, at any rate, an almost complete separation of the cortical "sensorium" from the "motorium" (except certain "postural" movements found by Graham Brown, Vogt, and Föerster when the postcentral cortex was stimulated) must, therefore, be replaced by another and a more appropriate conception. It would, however, be an error to return to the former viewpoint of the integral unitarians by declaring the entire extensive precentral-postcentral region as a sensory-motor mechanism, the "sensomotorium" of Exner, Munk, and others, everywhere uniformly organized and functionally equivalent. Certainly the findings of the students of cortical cytoarchitecture and myeloarchitecture, whose division of the Rolandic region into several areas cannot reasonably be disputed, are opposed to such a view. Also the present finding of differences in the number and course of the

intracortical afferent fibers in various areas of the extensive somatic sensory cortex are in perfect accord with, and would tend to support, the division of the whole central region into several distinct areas more or less parallel with the sulcus centralis. This also agrees with what has been said on the segmentation of the thalamus and of the thalamo-cortical radiation. All this indicates a functional differentiation of the whole extensive precentral-postcentral somato-sensory region into several suborgans whose functions cannot be regarded as identical. For the same reason the conception of the precentral cortex as an "accessory" to the "main" postcentral somato-sensory region is also not acceptable, although a close collaboration of all the mentioned suborgans is more than probable. The question which arises here is: What particular somato-sensory function must be localized in the precentral cortex, and what other forms or qualities of sensibility are connected with the postcentral region? So far, the clinical and the experimental investigations have, beyond a few hints, been unable to give a clear answer to this question, the majority of modern neurologists entirely dismissing the precentral cortex as a possible somato-sensory region. Ransom and Cushing (1909, p. 48 [7]) in reporting certain sensations of a proprioceptive character when the precentral cortex in a conscious subject was stimulated without movements being seen, remain alone; while Foerster (1927) in his extensive studies, also with conscious subjects, and recently Mankowski (1929) in the same way, evoked both proprioceptive and exteroceptive forms of sensation exclusively when the postcentral-parietal region was stimulated. Minkowski (1917, 1924), in discussing his experiments with monkeys where the precentral region was removed and sensory changes of a proprioceptive character noticed, expressed the opinion that a special form of proprioceptive sensibility, the "unconscious reflex sensibility," might be localized in the precentral cortex hitherto regarded as purely motor. (See also Bastian and Monakow, 1914, pp. 252, 276, 295, 298.) Dusser de Barenne's experiments with monkeys also point toward a certain somato-sensory function of the "motor" cortex. Foerster (1925, 1927) in connection with the above mentioned experiments supposes that the precentral cortex may play the rôle of an "accessory somato-sensory region" acting in a vicarious way in case the postcentral "main somato-sensory region" is damaged. The question of the form or quality of the sensibility to be attributed to the precentral cortex is closely connected with another problem; namely, whether different forms of sensibility are represented in different cytoarchitectural areas or perhaps in different layers of the

entire somato-sensory cortex. So far neither experimental studies with animals and with conscious patients nor pathological clinical investigations have brought that problem nearer to its solution. (Vogt, [1919] has made probable that in certain motor performances of the precentral gigantopyramidal area there is a collaboration of all cortical layers of this area or a portion of it in producing special motor acts.) The previous cytoarchitectural studies and the areal and regional differences in the character of the intracortical afferent fibers found in the present investigations harmonize rather well with the assumption of areal and regional differences in the function of the somato-sensory cortex. According to my view, each precentral and postcentral cytoarchitectural area would be endowed with its own special component of a primitive, elementary quality of sensibility not identical with that of the other somato-sensory areas. (Whether these primitive qualities are identical with those distinguished by physiology, psychology, and pathology has to be determined by further experimental investigation, by separate ablation of definite cytoarchitectural areas, and by clinical and pathological investigations.) Yet this would in no way exclude the possibility that in the subjective realization of a special form of sensation the rôles of certain cell layers of a given area would be different. (Compare also Vogt, 1919, p. 440.) In other words, for the subjective experience of different forms of somatic sensation cortical elements differing in shape, size, number, distribution, and connections are required. Thus, by way of hypothesis, the granular layer of the postcentral cortex would be indispensable for the exteroceptive forms of somatic sensation and that form of proprioceptive sensibility bearing a more conscious character; the agranular precentral cortex, on the other hand, would be subservient to a form of the proprioceptive sensibility remaining largely unconscious. Such an assumption of differences in receptive function between the precentral and the postcentral region would also be in good accord with Vogt's (1919, p. 458), Flechsig's (1920, pp. 18, 38), and Minkowski's (1923-24) findings of the differences in connections between the precentral and the postcentral regions. According to Vogt, the precentral area 4 is related to the anterior portion of the thalamus where tegmento-thalamic fibers terminate, while the postcentral region receives fibers from the posterior portion of the thalamus where the median fillet terminates. (Compare also Quensel, 1909, 1910; Meyer-Müller, Tsunesuke Fukuda, Flechsig, 1927, pp. 79, 80, 81, 111, and Bonhoeffer, 1928.)

Considering the results of the present investigations it might be easier to understand what obstacles until now have prevented a satis-

factory explanation of the cortical somatic sensory function. As has been shown, the "nuclear or focal zone" of the somatic sensory cortex in the monkey's brain, and possibly in man's as well (areas PA and PB of Economo-Koskinas), does not correspond with the convexities of either the postcentral or the precentral convolutions, but is entirely sunk in the sulcus centralis. By reason of the close proximity of the "focal zone" and the postcentral cortex in general, which seems to be essentially a conscious exteroceptive and probably conscious proprioceptive mechanism, in the experiments where an attempt was made to remove the precentral cortex separately, and in similar pathological cases, occasionally some impairment of exteroceptive sensibility was registered, suggesting a localization of that form of sensibility in the precentral "motor" cortex. In other experiments and analogous pathological cases where the injury of the precentral cortex was sufficiently far away from the "focal zone," symptoms not bearing the conscious exteroceptive character and due to the peculiar character of the "unconscious reflex sensibility" localized here, were not properly recognized and the rôle of the precentral cortex in any form of sensation was altogether denied. This problem appears to be well within the sphere of the technical possibility of attack in an experimental way, by injuries strictly limited to one or to a few adjoining cytoarchitectural areas without injury to the subcortical substance, as it will be shown in one of further reports. (Compare fig. 77.)

Taken all together, the present investigations clearly demonstrate that some form or other of the receptive, somato-sensory function has to be attributed also to the precentral agranular cortex. It is, however, a task for further physiological and clinical investigation to disclose the true nature of the sensibility which must be localized in this cortex. In carefully conducted experiments, when removing the precentral cortex, special attention must be paid to the "focal zone" and its portion of the thalamo-cortical radiation. Further, if the present anatomical experiments are repeated, the transverse segmentation of the thalamo-cortical radiation must be considered; otherwise, if either the posterior or the anterior fiber "fan" of the radiation alone were interrupted and if the conclusion were drawn that the entire thalamo-cortical radiation terminates in the postcentral region only, or in the precentral region only, one would commit the same error as some previous investigators. To obtain reliable and satisfactory results it will be indispensable to produce as complete degeneration as possible of the entire radiation.

CHAPTER IX

RESULTS OF THE PRESENT INVESTIGATIONS OF THE
SOMATIC SENSORY SYSTEMS1. AFFERENT SOMATO-SENSORY TRACTS FROM LOWER
REGIONS OF THE NEURAXIS TO THE THALAMUS

The first question to be answered in regard to the somato-sensory system is the relation between the afferent fiber tracts from the spinal cord, bulb, pons, and cerebellum, and the thalamus. Contrary to the prevalent view that only the ventral nucleus of the thalamus, or that nucleus preponderantly, must be regarded as the terminal region of the above mentioned tracts, the present experiments show clearly the spreading of these fibers almost over the entire ventro-lateral and dorso-lateral nucleus, as far dorsally as the vicinity of the caudate nucleus. Thus the entire lateral and larger portion of the thalamus receives afferent impulses from the periphery. Moreover, the lateral nucleus receives afferent fibers in its entire transverse extent or width, that is, in the whole region situated between the internal and external medullary laminae and not merely in a narrow zone along the external lamina, as commonly believed. Further it is important in understanding the internal organization and function of the entire somatic sensory system to know that the afferent fibers entering the thalamus do not spread here in an irregular or "diffuse" fashion. The course of these fibers and fiber bundles is fairly regular and parallel to the lateral contour of the thalamus, bundle alongside of bundle. This already indicates a definite, orderly, or "spatial" arrangement of special portions or subsystems of the intermediate somato-sensory tracts and a morphological and functional segmentation of the thalamus. No evidence was found to support the belief in the existence of a "through" or "cortical" lemniscus which would merely pass the thalamus on its way to the cortex or to subcortical basal nuclei. The course of all the incoming somato-sensory fibers in the thalamus is approximately vertical, cutting at a right angle the horizontal bundles which are the outgoing thalamo-cortical fibers. This can be explained only by accepting the termination in the thalamus of all or at any rate, the majority of the somatic sensory fibers from lower regions of the neuraxis. Whether, nevertheless, some fibers pass the thalamus to

terminate in the basal nuclei and in the cerebral cortex as alleged, must be studied by other experiments. There are indications that the medial nucleus of the thalamus receives a part of the intermediate somato-sensory tracts by way of the internal medullary lamina. But no evidence was found that any such fibers terminate in the so-called dorsal or anterior nucleus.

2. DESCENDING CORTICO-THALAMIC AND OTHER CORTICO-FUGAL FIBERS

The existence of an extensive descending cortico-thalamic fiber system, which according to some investigators plays an important rôle in normal and in pathological somato-sensory function (Head, Wallenberg, see also Long, Mellus, Ramón y Cajal, Probst, Hollander, Villaverde, and my paper, 1926), cannot definitely be denied, although fibers of this character are somewhat more numerous only in the most ventral zone of the ventro-lateral nucleus. (See also Minkowski, 1923-24, and Riese, 1925.)

The bulk of the fibers which degenerate after the destruction of the occipito-parietal cortex and enter the caudal portion of the thalamus, especially the pulvinar, certainly reach the midbrain by way of the brachium of the superior colliculus. (In Experiment XV, figs. 95, 96, not further reported here, the area peri-parastriata of Elliot Smith, areas 18 and 19 of Brodmann, or field 19-a of Vogt was destroyed; whether some of these fibers may, nevertheless, terminate in the thalamus or give off collaterals during their passage through the thalamus cannot be decided by Marchi's method and must be studied by Golgi's method in higher mammals and in man; scarcely any of these fibers originate in the area striata itself, see figs. 86-94 of Experiment XIV.) This fact, together with the findings of Brouwer and Zeeman, and of Overbosch,—that no peripheral afferent optic fibers enter the thalamus (pulvinar),—militates against the view which regards both the thalamus and midbrain as subcortical stations for the cortico-petal visual impulses. (Compare Visual System).

Other numerous cortico-fugal fibers descending from the precentral and frontal cortical regions (both regions are taken as a unit; a detailed analysis of these different tracts according to areas will be given at a later time), are:

(1) very numerous and quite fine fibers to the caudate nucleus (tractus cortico-caudatus) by way of the subcallosal stratum and the

internal capsule (fig. 44 of Experiment II, fig. 78 of Experiment VII, figs. 80, 81, 83 of Experiment VIII, fig. 85 of Experiment IX);

(2) also numerous yet somewhat stronger fibers to the globus pallidus entering it by its dorsal extremity (tractus cortico-pallidalis, figs. 78, 79 of Experiment VII, figs. 81, 82 of Experiment VIII);

(3) fairly thin fibers to the red nucleus (tractus cortico-rubralis, fig. 85 of Experiment IX), and

(4) also fairly strong and medium sized fibers in considerable numbers to the stratum intermedium of the peduncle and to the substantia nigra of Soemmering (tractus cortico-peduncularis and cortico-nigralis), as far caudalward as the substantia nigra extends, descending partly by way of the median fillet (figs. 83, 84 of Experiment VIII). (Thus the substantia nigra and the neighboring grey matter appear as an important subcortical motor mechanism being under a direct influence of the frontal-precentral cortex; this explains the absence of changes in the nigral cells in experiments where the frontal cortex alone was removed);

(5) besides the well-known cortico-spinal, cortico-bulbar, and numerous associational and callosal fibers.

3. SOMATO-SENSORY RADIATION

Primary interest in this investigation was focused on the origin, course, and termination of the thalamo-cortical radiation. It was found that these fibers (*sr* in corresponding figures), originate from the entire lateral nucleus of the thalamus, that is, from both the ventro-lateral and the dorso-lateral nucleus as far dorsally as the neighborhood of the caudate nucleus, and not just from the narrow lateral zone of the ventro-lateral nucleus. In a word, it is at least the lateral nucleus of the thalamus in its entire dorso-ventral and medio-lateral extent situated between both medullary laminae which is the terminal station for the lower ascending somatic sensory tracts as well as the point of departure of the uppermost link of the afferent somatic sensory system, the thalamo-cortical radiation. (Compare Flechsig, 1920, p. 28.) This thalamic radiation is a huge fiber system which uses not only the posterior limb but to a certain extent as well, the anterior limb of the internal capsule on its way to the cortex. In the internal capsule at the level of the caudate nucleus all more caudal thalamo-cortical fibers converge and come to lie close together since here they all must pass the relatively narrow space between the caudate

nucleus and the thalamus on the one hand, and the putamen and Sylvian fossa on the other. At this spot the entire sensory radiation can easily be interrupted by a relatively small lesion; whereas below that spot in the ventral portion of the internal capsule and in the thalamus itself, as also above it in the centrum semiovale, the fascicles of the somato-sensory radiation diverge from one another. The thalamo-cortical radiation can be imagined as composed of individual fiber segments or sheets ("fans") arranged in a certain definite way. Bundles, or fans originating from the caudal portion of the thalamus occupy a caudal position in the radiation; those from the rostral portion remain anterior in the radiation; this indicates a transverse segmentation of the sensory radiation perpendicular to the long axis of the hemisphere and thalamus. Other factors indicate a longitudinal segmentation of the radiation wherein the fascicles from the dorsal portion of the lateral nucleus reach the dorsal zones of the somato-sensory cortex, and those from the ventral portions of the lateral nucleus reach the ventral zones of that cortex. On the one hand, this would explain the functional segmentation of the thalamus, and, on the other hand, could be related to the cytoarchitectural and functional segmentation of the somato-sensory cortex into several parallel areas along the sulcus centralis. Also such a regular or "spatial" arrangement of the thalamo-cortical radiation, together with what is known of the composition of the lower links of the somatic sensory paths, and what is known from physiological, clinical, and pathological observations of the projection of the peripheral receptive surface of the body upon the somato-sensory cortex, the so-called somato-topic cortical representation of the body (compare Cushing, 1909; Valkenburg, 1914; Vogt, 1919; Foerster, 1927; and Mankowski, 1929), suggests the mechanisms underlying that property of the somato-sensory function called "localization" or spatial discrimination (see also Henschen, 1918, p. 456). But here further detailed investigation is necessary. (Compare Chapter XIX.)

Another feature of the thalamo-cortical radiation is the strictly unilateral course of that entire fiber system. No fibers which would cross to the opposite hemisphere by way of the corpus callosum, contrary to the supposition of some investigators, were seen in any of the examined series where the thalamus alone or the internal capsule alone was injured. They show not the slightest tendency to turn into the corpus callosum although those fibers which spring from the most dorsal portion of the dorso-lateral nucleus close to the caudate nucleus

were also interrupted; and it was these fibers especially for which such a decussation was claimed. If there should exist a bilateral cortical somato-sensory representation of certain portions of the body (regions near the median line), an assumption otherwise not very probable, a partial re-crossing of the afferent somato-sensory tracts must be achieved at levels below the thalamus or in the thalamus itself (see Wallenberg). At any rate, the "sparing" of the sensibility of such peripheral regions of the body in cases of hemianaesthesia cannot be explained by a re-crossing of a portion of the thalamo-cortical radiation; it is due rather to a sheltered position of portions of the thalamo-cortical radiation in question and of the corresponding cortical representations. (Compare the explanation of the preservation of "central" or macular vision, Visual System.)

4. BOUNDARIES OF THE SOMATO-SENSORY PROJECTION CORTEX

Apparently the most important result in the present investigations is that concerning the extent or boundaries of the somato-sensory cortex (shaded areas on both sides of the sulcus centralis *C* and around the sulcus cinguli *Sc* in fig. 6.) A careful tracing of the degenerated thalamic fibers up to their cortical terminations showed that unquestionably the somato-sensory cortex does not merely occupy a narrow strip, perhaps corresponding only with Brodmann's areas 1, 2, and 3, stretching immediately behind and buried in the sulcus centralis (fig. 7), as accepted by almost all authorities at the present time. In fact, the somatic sensory cortex occupies the entire precentral agranular region and a considerable portion of the parietal granular region, in addition to the entire postcentral granular region. In particular, the somatic sensory cortex extends over Brodmann's areas 1, 2, 3, 4, 5, 6, 43, and the oral portion of area 7. In view of the long continued dispute on the real functional significance of the precentral region, especially of the so-called motor region or the area praecentralis gigantopyramidalis, area 4 of Brodmann, particular attention was paid to the afferent fibers of that area. There cannot be, however, any doubt that both areas 4 and 6 of Brodmann receive numerous afferent fibers, which were traced from their thalamic origin up to and into the precentral cortex. However, certain differences exist as to the numerical distribution of somato-sensory fibers to various cytoarchitectural areas of the extensive pre- and postcentral somato-sensory cortex. There are also features different and peculiar to each area, besides other

characteristics which are common to all. The densest bundles of the thalamo-cortical radiation enter the cortex lining the floor of the sulcus centralis and its immediate vicinity along both walls of that sulcus. The number of afferent fibers gradually decreases toward both lips of the central sulcus belonging to both precentral and postcentral convolutions. Since, according to cytoarchitectural investigations, the postcentral granular type of the cortex, besides occupying the whole postcentral region (that is, the convexity of the postcentral convolution and the posterior wall of the sulcus centralis), pushes out for a short distance to the anterior wall of the sulcus centralis, it is more than probable that the zone which, according to the present investigations, receives the most abundant afferent fiber supply in the entire somato-sensory cortex, is identical with the most anterior narrow strip of the postcentral cortex around the fundus of the sulcus centralis, where the inner granular layer has also its best development (area 3 of Brodmann). This zone must, therefore, be considered as the "nuclear or focal zone" of the entire somato-sensory region of the hemisphere (deeply shaded, narrow areas on both sides of the sulcus centralis *C* in fig. 6, in reality entirely sunk in the sulcus). The number of the afferent fibers, as has been said, decreases gradually in both the anterior and posterior walls of the central sulcus toward the convexities of the precentral and postcentral convolutions. This slow and gradual decrease does not, however, show any particular difference between the two walls. A further decrease is noticeable in the cortex covering the convexities of both the central convolutions. Thus the areas 1, 2, and 4 of Brodmann (wider doubly shaded areas in front and behind the sulcus centralis in fig. 6) being about equally supplied with the afferent fibers, though less abundantly than the "focal zone" around the bottom of the sulcus centralis (area 3 of Brodmann), form a belt in front of and behind the "focal zone." However, in all three areas mentioned which do not belong to the "focal zone" the number of afferent fibers is still quite considerable. In front of area 4 and behind the postcentral region there is the third or outer belt of the somato-sensory cortex where the number of sensory fibers shows a further gradual decrease until their complete disappearance toward the fringes of the somato-sensory region (areas 6, 5, and the oral portion of area 7, lightly shaded areas in fig. 6). Area 6 is nevertheless almost entirely included in this region. On the internal face of the hemisphere the somatic sensory cortex extends as far as the sulcus cinguli (*Sc* in fig. 6), and occupies about the same areas as on the

external face. In its posterior portion the somato-sensory cortex even overlaps for a short distance areas 23 and 24 of Brodmann. It is fairly safe to accept the caudal boundaries of the somatic sensory cortex in the parietal lobe determined here as closely approaching the existing limits of that cortex. The same certainty does not exist with regard to the anterior boundary; and the possibility cannot be excluded that a portion of the thalamo-cortical radiation springing from the anterior thalamic segment might spread more orally over the frontal lobe. This particular question must be investigated by special experiments. At any rate, the extent of the somatic sensory cortex as found in these investigations must be recognized as the "minimal" somatic sensory region of the hemisphere.

5. CORTICAL TERMINATIONS OF THE SOMATO-SENSORY AFFERENT FIBERS

A feature common to all intracortical terminations of afferent fibers both in the precentral and in the postcentral cortex is: a somewhat irregular course seldom corresponding with the regularly arranged vertical "radiated bundles," the latter being the entering and outgoing association, callosal, and efferent fibers. For the most part the exogenous afferent fibers have an oblique ascending course through the lower strata of the cortex toward both stripes of Baillarger. In the voluminous precentral cortex the degenerated afferent fibers usually have, for long stretches, a somewhat straighter course and ascend directly from the subcortical white substance, cutting at sharp angles the actual "radiated bundles." In the thinner postcentral cortex the exogenous afferent fibers ascend more gradually toward the stripes of Baillarger, many fibers exhibiting here a horizontal direction, more or less parallel with the cortical layers. Everywhere the afferent fibers reach the lower stripe of Baillarger with many fine fiber segments penetrating into the lamina interstriata and reach the upper stripe of Baillarger. Both stripes of Baillarger, especially in the cortex of the bottom of the sulcus centralis, are filled with countless fine, and a few somewhat coarser, blackened particles and detritus of the disintegrated myelin and with short segments of degenerated fibers. This is considerably less pronounced or entirely absent in the cortex covering the convexities of both the precentral and postcentral convolutions. A few delicate and fairly long horizontal degenerated fibers were also seen in the region of the stripes of Baillarger itself. In the upper

strata of the cortex above the upper stripe of Baillarger a few fine exogenous afferent fibers were seen also but only in the cortex around the bottom of the sulcus centralis, these being absent in the convexities of both central convolutions. From the above findings it is evident that the coarse, oblique, and horizontal fibers of both the precentral and the postcentral convolutions and of the sulcus centralis, described by the students of the cortical myeloarchitecture in the lower layers (compare Vogt, 1919), are exogenous afferent thalamo-cortical fibers mostly quite distinct from the actual "radiated fibers" and identical with the exogenous somato-sensory fibers of Ramón y Cajal (who found them, however, in the precentral cortex only, see Ramón y Cajal, 1909-11, vol. II, pp. 576, 584, 640-643, 646, 829) and of Flechsig (1920, pp. 16, 17). These exogeneous thalamic fibers form a part of the so-called "basal meshwork" ("Grundfaserfilz" of Vogt) discernible between the "radiated fibers" in the lower cortical layers. These peculiarities of the afferent somato-sensory fibers are comparable to those of the intra-cortical afferent visual fibers of the striate area. Further, it should be mentioned that the supply of the afferent fibers to the somatic sensory cortex is continuous, at least in the cortex around the sulcus centralis, at which spot dense bundles of degenerated fibers enter the cortex. Here, at any rate, there are no small cortical islets, supplied with afferent fibers and separated from each other by narrow zones devoid of such a supply; this negative feature characterizes likewise the striate area.

6. FUNCTION OF THE SOMATO-SENSORY PROJECTION CORTEX

The present experiments demonstrate that the somato-sensory cortex extends to both sides of the central sulcus occupying the precentral region and a portion of the parietal region, besides the postcentral region of the students of the cortical cytoarchitecture. Since each of the regions mentioned receives afferent impulses by way of its own fibers and since this is probable also with respect to each of the individual cytoarchitectural areas, it must be assumed that the extensive somato-sensory region is a composite cortical organ consisting of a considerable number of suborgans, each of them with its own specific receptive function (besides various efferent and other functions). The special receptive function of each precentral-postcentral and parietal area must be determined by further investigations.

PART II
AUDITORY SYSTEM

CHAPTER X

ORIGIN, COURSE, TERMINATION, AND INTERNAL ORGANIZATION OF THE AUDITORY RADIATION

In two of the reported experiments (Experiment I and II) fibers forming the auditory radiation, besides the thalamo-cortical radiation described in the foregoing chapters, and the visual radiation to be described later, were interrupted and degenerated.

In Experiment I by the lesion described previously (see Chapter V) the internal geniculate body (*Cgm* in corresponding figures) was partly destroyed directly and partly separated from the hemisphere (figs. 33-35). In Experiment II the internal geniculate body was also directly destroyed, but in addition the auditory radiation was completely interrupted close to its origin (figs. 51, 52, especially fig. 51). In both experiments the auditory radiation (*ar* in corresponding figures) apparently degenerated completely, particularly in Experiment II, thus rendering it possible to trace the entire course of the radiation from its origin to its termination in the cortex of the Sylvian fossa (figs. 26-31, 33, 34 and figs. 47-51, and perhaps *x* in figs. 52-54).

Since in both experiments the findings are nearly identical, the description given here is the result of both experiments.

The course of the auditory radiation (*ar* in accompanying figures), is as follows: From the internal geniculate body a strong bundle of closely assembled degenerated fibers turns in a light arc laterally, entering the most ventral portion of the internal capsule immediately above the lateral geniculate body (*Cgl* in figs. 30, 31, 33, 51). Near their origin while still within the between-brain, but also in the internal capsule, it is not easy to distinguish between the auditory and the ventral somatic sensory fibers, the latter originating from the most ventral portion of the thalamus and forming the ventral bundles of the thalamo-cortical radiation (figs. 30-32, 51; compare Chapter V). The majority of the auditory fibers, however, form one single strong bundle or rather a fiber lamina, having nearly a horizontal position. Both somatic sensory and auditory fibers can be kept apart better more laterally toward the putamen where they diverge from one another. Ventral somatic sensory bundles soon after they enter the

internal capsule turn dorsally in their ascending course along the inner border of the putamen and partly also through the latter nucleus, as described before. Auditory fibers remaining horizontal or bending slightly ventralward reach the external capsule by penetrating through the ventral edge of the posterior portion of the putamen. Besides, the single strong bundle of the auditory radiation while still within the internal capsule, has on frontal sections through the hemisphere a characteristic appearance (figs. 30, 31, 33, 51). It is composed of short oblique fiber segments arranged in a fairly regular way side by side, thus making in reality a thick, dense fiber lamina, which forms above the oral portion of the lateral geniculate body a cap or a capsule. Practically all auditory fibers cross the ventral region of the internal capsule in front of the plane where the central visual path appears as the triangular field of Wernicke and gradually changes its shape into the sagittal layers of the temporo-parietal lobes. Hardly any of the auditory fibers pass through the visual radiation itself. Thus both the visual and the auditory geniculo-cortical radiations, although lying close together, are separated; the auditory radiation being more frontal, crosses at a right angle above the visual radiation, while the latter takes a sagittal direction occipitalward. Arriving at the internal contour of the putamen, the majority of auditory fibers penetrate through the substance of that nucleus as strong or thin fiber bundles in order to reach the external capsule, thus dividing the ventral portion of the posterior putamen into several islets in exactly the same way as has been described for the ventral thalamo-cortical fiber bundles in relation to the dorsal ridge of the posterior putamen (figs. 29-32, 50, 51). Many bundles of the auditory radiation turn around the posterior edge of the putamen (figs. 33, 34). Within the external capsule (figs. 32-34) auditory fibers are to some extent mingled with other fibers arriving from the ventral thalamic region, the latter ascending here dorsalward (on the real functional significance of these latter fibers, *x* in figs. 52-54, nothing definite can be said at present; see Chapters V, VI, and Chapter XI, 2). Here pass also other fibers belonging to the anterior commissure and to various association systems. Reaching the white substance of the superior temporal convolution (T_1), auditory fibers proceed laterally along the cortex of the dorsal lip of this convolution; that is, some close beneath the floor of the Sylvian fossa (*FS*), some through the ventral spur of the claustrum. Generally, all fibers of the auditory radiation, with a few exceptions, are strictly confined to the upper or

dorsal half of the white substance of the superior temporal convolution close to the cortex of the lower wall of the Sylvian fossa, and along and within the ventral spur of the claustrum, leaving the ventral half of the white substance for the most part entirely free (compare a similar behavior of the visual fibers, Chapter XV). At this spot, too, in so far as the auditory fibers do not enter the cortex immediately, they can be seen as short, more or less parallel, oblique, or somewhat obliquely horizontally arranged fiber segments, forming a thin fiber sheet or lamina, each section of the series showing a few fibers which actually enter the cortex on the corresponding level. The overwhelming majority of the auditory fibers gradually enter the cortex of the covered dorsal lip of the superior temporal convolution (T_1) or, in other words, the ventral horizontal wall of the Sylvian fossa (FS). Only a few solitary fibers reach the convexity of the superior temporal convolution on the free face of the temporal lobe. No auditory fibers in any of the present experiments were seen to enter the lower, ventral lip of the superior temporal convolution around the superior temporal sulcus (St_1) or any other part of the cortex of the temporal lobe (for example the middle or the inferior temporal convolution).

Some of the auditory fibers (also some of the ventral somato-sensory fibers) do not observe this course in the external capsule and penetrate through the claustrum into the capsula extrema (fig. 33). From the capsula extrema they either enter the medial (perpendicular) wall of the Sylvian fossa along the claustrum or turn around and below the ventral corner of the fossa eventually entering the covered portion of the insulo-temporal cortex. Thus all the fibers forming the auditory radiation, as the close study of both series demonstrates, no matter whether penetrating directly through or avoiding the putamen from behind, finally reach the Sylvian fossa and the hidden upper lip of the superior temporal convolution.

In more oral sections where the putamen increases in size before, however, attaining its greatest extent, all fibers of the auditory radiation have already passed over to the external capsule (*ar* in figs. 28, 29, 48, 49). From then on, they can be found on anterior levels only lateral to the putamen and constitute at that spot a portion of the "sagittal stratum" of the temporal lobe immediately neighboring the ventral extremity of the claustrum. From the sagittal layer where they run for a longer or shorter distance in a longitudinal direction, the auditory fibers deviate laterally in a definite order, bundle after bundle, to reach their respective places of termination in the more orally situated segments of the auditory projection cortex. First the

most dorsal and at the same time the most caudal bundles turn laterally into the upper lip of the superior temporal convolution which here, in the posterior corner of the Sylvian fossa, shows an elevation comparable to the transverse convolution of Heschl in the human brain (*Ttr* in figs 30, 50, 51). Farther on orally, the successive ventral bundles, these being at the same time more rostral, turn toward the upper lip of the superior temporal convolution, and toward its successive rostral segments. Accordingly, the ventral bundles of the auditory radiation run for a short stretch in the sagittal direction as the sagittal stratum. The longest sagittal course is taken by the most oral-ventral bundles running to the most oral portions or segments of the auditory projection cortex, and the shortest course by the postero-dorsal bundles destined for the posterior or caudal segments of the auditory projection cortex around the posterior corner of the Sylvian fossa. It is, therefore, easy to understand why the same bundles appear on certain sections as cross-sectioned bundles of the sagittal stratum, while on others they appear as long fibers taking a transverse direction in the white substance of the superior temporal convolution. These transversely running fibers were naturally found in greater numbers in sections corresponding with the posterior region of the Sylvian fossa, in small numbers in sections through anterior planes. Fibers which do not reach directly the posterior segment of the auditory projection cortex coating the most posterior portion of the Sylvian fossa, do so gradually as they approach the more orally situated portion of the same cortex. The more anterior sections of the series show a gradual decrease in the number of degenerated auditory fibers until they completely disappear (*ar* in figs. 26, 27 and 47, 48).

The regular arrangement and distribution of fibers of the auditory radiation during their course toward the cortex is remarkable, especially in the white substance beneath the Sylvian fossa. Here, as well as in the internal capsule, they almost all lie apparently parallel to one another, excepting such fibers as leave their common fiber layer to enter various segments of the auditory projection cortex. The entire auditory radiation, accordingly, represents a thin, regularly arranged fiber system or lamina whose shape resembles that of an irregular "fan," the radii of which are represented by individual fibers and fiber bundles. These radii or ribs of the fan are, close to their origin within the internal geniculate body, closely assembled into one single bundle ("handle" of the fan) gradually diverging as they approach the cortex. Consequently, the radii or bundles composing the auditory radiation are not mixed one with another in an irregular way. Each

of them preserves its relative position with respect to its neighbor during its entire course up to its cortical termination. In particular, the dorsal and at the same time the most caudal bundles of the auditory radiation are destined for the most caudal segments of the auditory projection cortex coating the posterior corner of the Sylvian fossa. The most ventral and at the same time the most oral bundles of the radiation reach the most oral or rostral segments of the auditory projection cortex. The remaining intermediate bundles are distributed in a regular way to intermediate segments of that cortex. From such an arrangement of the fibers of the auditory radiation, it is permissible to suppose a similar arrangement of the individual segments of the auditory projection cortex paralleling one another and strung along a line approximately parallel to the long axis of the superior temporal convolution (in the human brain somewhat obliquely across the posterior Sylvian fossa corresponding to the axis of the transverse temporal convolution of Heschl).

The fiber fan or the lamina formed by the auditory radiation shows, in addition to the above features, another peculiarity. The anterior or oral ribs of that fan are lowered ventrally, and the posterior ribs lifted a little dorsalward, thus indicating a spiral rotation of the radiation for approximately ninety degrees around one of the central ribs or radii (compare Pfeifer, 1920). This can be explained by the auditory fiber lamina being at the point of its cortical termination originally situated in a vertical or nearly vertical position, corresponding with the planes vertical to the long axis of the hemisphere, and with the oblong auditory projection cortex also having originally an almost perpendicular position (gyrus sylvius in carnivora for example). With the changing of the position of this cortical region into one more horizontal-longitudinal, as encountered in primates, the lateral portion of the auditory fiber lamina where it leans toward the cortex also gradually came to occupy a more horizontal position approximately parallel to the lower or ventral wall of the Sylvian fossa; the bundles of the auditory radiation originally ventral, becoming more oral or rostral; and the bundles originally dorsal, remaining or becoming caudal. This rotation of the auditory radiation as described, seems to have been attained in greater degree closer to the cortex, while its portion nearer the internal geniculate body has accomplished a lesser rotation. In addition to this transverse rotation of the auditory radiation another point must be considered: the shifting of the internal geniculate body from its original ventral position to an internal position in relation to the external geniculate body; that is, the rotation

of the epithalamus around a longitudinal axis. The first of the peculiarities of the auditory radiation, as described, the consequence of phylo- and ontogenetic factors, indicates an incomplete rotation of that fiber system in the sense of a spiral around a transverse axis which can be imagined as extending from the internal geniculate body to the temporal cortex. The second rotation is evidenced by the obliquely sectioned fibers of the "handle" of the auditory radiation near the external geniculate body (see accompanying figures). We can look upon the cause of this rotation of the radiation, as it appears in the adult brain of primates, as an adaptation to the changed conditions as compared with that in lower mammals. Its only interpretation, however, must be the necessary preservation of the original mutual relations of the individual bundles and fibers of the radiation to one another and above all to special segments of the internal geniculate body and the auditory projection cortex. And this in turn renders possible an exact projection of the receptor surface of the auditory peripheral organ, the cochlea, upon the auditory projection cortex. (Compare Chapters XII, XIX.)

The caliber of most of the central auditory fibers is fairly large and is hardly inferior to that of the coarse somatic sensory (thalamo-cortical) elements. Yet there are also fibers of a medium size and even a small number that are fairly thin. It would be of importance to know if there are regional differences in caliber, whether for instance, as seems to be the case, the fibers supplying the most anterior (rostral) segments of the auditory projection cortex are of smaller size than the fibers entering the most posterior (caudal) segments of that cortex. This would be important since the "representation" of low tones is claimed to be in the oral-lateral segments, and of the high tones in the caudal-medial segments of the auditory projection cortex. (Compare also different size of cells of the spiral ganglion corresponding to different segments of the cochlea, my paper, 1926.)

The absolute number of fibers of the entire auditory radiation, though considerable, is below that of the visual radiation and is considerably smaller than the number of fibers forming the somatic sensory (thalamo-cortical) radiation, which well harmonizes with the difference in size of the peripheral receptive surfaces: of the cochlea (papilla basilaris), of the retina, and of the surface of the body, muscles, joints, etc.

No evidence was found in support of a partial crossing or recrossing of the auditory radiation to the opposite hemisphere by way of the corpus callosum.

CHAPTER XI

LOCATION, EXTENT, AND FUNCTION OF THE AUDITORY
CORTEX1. BOUNDARIES OF THE AUDITORY PROJECTION CORTEX, CORTICAL
TERMINATIONS OF THE AUDITORY FIBERS

The relation of the afferent auditory fibers to the cortex of the hemisphere was determined in both of the present Experiments I and II with a fair degree of exactness. Not considering the relation to the claustrum (the possible branching of auditory fibers in that formation can naturally be ascertained only by Golgi's method), there can

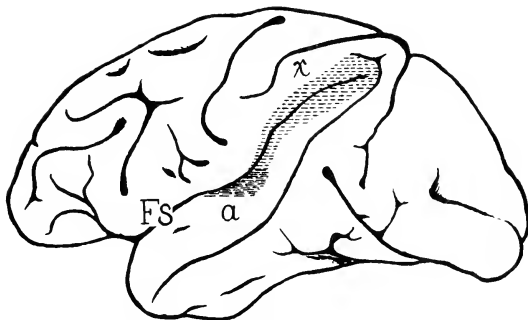


Fig. 10. A diagram showing the position of the auditory projection cortex in the brain of the monkey as determined in the present investigation (small deeply shaded area *a* below the Sylvian sulcus *FS*), and the posterior Sylvian projection area with as yet unknown significance (lightly shaded area *x* on both sides of the posterior extremity of the Sylvian sulcus). In reality both areas are for the most part submerged in the fissures, small portions only appearing on the free face of the hemisphere. Thus the shaded areas in the figure show more the location of these areas within the Sylvian fissure and their longitudinal extent. Note the extensive region of the temporal lobe which does not receive any afferent fibers. (Compare with figs. 7, 24.)

be no doubt that only the superior temporal convolution in its upper lip, corresponding with the lower or ventral horizontal wall of the Sylvian fossa, receives fibers of the auditory radiation, while only a few fibers reach the convex face of that convolution. (As to the nature of afferent fibers entering the perpendicular internal wall of the Sylvian fossa and the posterior portion of the Sylvian sulcus it is premature as yet to speak; see next paragraph.) Therefore, only that

portion of the temporal cortex just mentioned can at present be regarded as the actual "auditory projection cortex." That region occupies, accordingly, the entire dorsal lip of the superior temporal convolution buried in the Sylvian fossa, representing in fact the ventral wall of that fossa. More orally, the auditory projection cortex is limited to approximately the internal half of the upper lip of the superior temporal convolution sunk in the Sylvian fossa. Besides that, it would appear that a portion of the convexity of the superior temporal convolution receives a certain number of auditory fibers, at least the portion near the posterior corner of the Sylvian fossa. Thus the auditory cortical projection area has its widest extent in its caudal portion, decreasing toward its oral or rostral end, where it covers only a narrow zone hidden entirely in the Sylvian fossa (small, deeply shaded area ventrally to the Sylvian fissure *FS* in fig. 1; area *a* in figs. 2, 10, and 24, indicating more the longitudinal extent of the auditory cortex than its extent over the free face of the hemisphere).

The possibility that the auditory projection cortex which receives direct peripheral impulses, is somewhat wider than that delimited in these investigations must be considered. The present delimitation of the cortical projection center of hearing in the monkey depends on the completeness of the degeneration of the auditory radiation which has been caused by the experimental lesion. Considering the shape and the location of the injury in Experiments I and II, it does not, on the one hand, seem probable that any considerable portion of the radiation was left unaltered, especially so in Experiment II (see figs. 50, 51), and on the other hand, that any other cortico-petal, e.g., callosal fibers degenerated. At any rate the delimitation as given here must be regarded as a "minimal" possible extent of the auditory projection cortex. Furthermore, the present experiments show the complete absence of other afferent fibers from the between-brain to any other portion of the convex face of the temporal lobe, a contention of some investigators.

Sections through the posterior portion of the auditory projection region show the cortex of the upper lip of the superior temporal convolution containing in its lower layers a multitude of fine and medium-sized degenerated afferent fibers approaching a fiber layer which corresponds well with the inner stripe of Baillarger of that cortical area as delimited by Brodman (figs. 50, 51; see also Vogt, 1919, fig. 59). In this area the number of intracortical afferent fibers is the largest in

the entire auditory projection cortex. The smallest number of such cortical terminations was found in the region corresponding with the most anterior segment of the auditory projection cortex. If this be taken as a criterion of the best and of the poorest supply of the auditory projection cortex with afferent fibers, its most caudal segment would represent its "focal zone."¹ However, even in this focal zone, the wealth of degenerated intracortical afferent fibers is below that found in the "focal zone" of the somatic sensory region around the bottom of the sulcus centralis. (See Chapter VII.)

It might also be of importance to mention that here, in the cortex of the auditory "focal zone," just as was described for the somatic sensory cortex and for the striate area, the supply of afferent fibers is a continuous one without any visible gaps or zones lacking afferent fibers. This indicates that here as well as in the somatic sensory cortex and in the striate area, there is the same uninterrupted cortical representation of the peripheral receptive surface (cochlea, skin, retina).

As to how conditions in the brain of lower primates compare with those known in man, the following may be said: In the sylvian region of the *Macacus* essentially the same conditions exist as in the human brain, although more simplified. In the most posterior portion of the monkey's Sylvian fossa, there exists an elevation of the cortex of the upper lip of the superior temporal convolution (*Ttr*) which could well be compared with Heschl's transverse convolution (figs. 30, 50, 51, less evident in figs. 29, 33). That region actually has, in the present experiments, the best supply of afferent fibers and it might well be a homologue of area TC and TD of *Economo-Koskinas*. Thus in the monkey there also exists a special portion of the auditory projection cortex well supplied with afferent fibers, entirely, or at least, chiefly hidden in the Sylvian fossa, and comparable to Brodmann's areas 41 and 42 in the human hemisphere, or to *Mauss'* areas 38 and 40 found in the higher apes. Yet it is questionable whether the entire auditory projection cortex as here delimited in the monkey's brain is homologous merely to Brodmann's areas 52, 41, and 42, approximately *Economo's* area TC of the human brain, or whether it also embraces portions of area 22, and corresponds to areas TA, TB, TC, and TD of *Economo-Koskinas* taken together, as appears probable. At any rate, it is highly probable from the present experiments that a wide cortical region concerned with the reception of peripheral auditory impulses does not exist, but a comparatively small portion of

¹ Compare Beck, 1929.

the entire temporal cortex, though it appears larger than the narrow strip covering the transverse temporal convolution. (Compare following paragraph.) Moreover, that region does not receive "diffuse," but well arranged and regularly distributed afferent fibers. By far the larger portion of the temporal lobe including a considerable portion of the superior temporal convolution does not, in fact, stand in direct connection with subcortical regions by means of the auditory or any other afferent fibers. It is evident that in the monkey Brodmann's and Mauss' area 22 can in no case in its totality, as is accepted at present, but only partly be homologous with the areas 41, 42, and 52 of the human brain (fig. 7). Although the cytoarchitectural studies were unable to distinguish in the monkey brain a special area corresponding to Heschl's transverse convolutions in man (TC of Economo-Koskinas), there can be no doubt that such an area exists in lower primates also. (Compare Economo-Koskinas, pp. 707, 708; Beek, 1929, p. 413, and 1930, p. 253, and Niessl von Mayendorf, 1930.)

The boundaries of the auditory projection cortex as determined by the present experiments are all the more remarkable since in Experiment II a greater part of the temporal lobe was severed from the rest of the hemisphere and yet only the auditory radiation, which has been described, degenerated.

The deep position of the auditory projection cortex in the posterior portion of the Sylvian fossa in the Macacus, rendering this furrow comparable to the calcarine fissure and to the central sulcus, accounts for the discrepancies observed in various physiological experiments. The anatomical experimental method of investigation—demonstrating as it clearly does the position and the extent of the terminal cortical area of the central auditory path—that has been used in the present experiments, can serve as a reliable basis for future physiological studies. (See Chapter XX.)

2. PROBABLE FUNCTIONAL SIGNIFICANCE OF THE POSTERIOR SYLVIAN RECEPTIVE REGION

There do not exist other dependable means, except physiological experiments, of determining what special function can be attributed to that region of the temporo-parietal cortex stretching from the immediate neighborhood of the undoubted auditory projection cortex (small deeply shaded area *a*) in an occipital direction as far as the posterior end of the Sylvian sulcus (lightly shaded area *x* in figs. 2, 10, and 24).

The fact that this new receptive area closely adjoins the actual auditory area would argue for a close onto- and phylogenetic and also a functional relationship to the eighth nerve. The same is suggested by the probable origin of fibers which reach that temporo-parietal region either from the internal geniculate body or from the ventral thalamic region or even from the hypothalamus, which fibers form in reality the caudal extension of the central auditory path. (Compare fig. 51 with fig. 52.) The possibility that these fibers originate in the dorso-lateral nucleus of the thalamus can almost certainly be excluded. Perhaps the more oral portion of that region belongs indeed to the cochlear projection cortex. The same can easily be true in respect to its more caudal portion. This would give a plausible explanation to the negative results of Schäfer (1888) who observed auditory functions unimpaired though the superior temporal convolution or even the entire temporal lobe was removed; in his experiments with monkeys this posterior Sylvian region remained undamaged. On the other hand, the close vicinity of a portion of that cortex to the corpus striatum makes us think that it may be somehow related to the sense of equilibrium. In considering such a possibility I have reference to the opinion of Spiller (1906) and of Ariens Kappers (1921). It would appear that the decision of this question can be reached by physiological experiments. It should not be difficult to destroy separately the cortex along both lips of the posterior extremity of the fissura Sylvii including the posterior portion of the Sylvian fossa in both hemispheres, and to examine what particular function is subsequently lost. (See also Chapter XIII.)

CHAPTER XII

AN ATTEMPT TO EXPLAIN THE MINUTE FUNCTION OF
THE AUDITORY SYSTEM

The first successful attempt to explain the nature of the subjective processes in audition with the help of structures of the inner ear was made sometime ago in the classic work of Helmholtz (1863). In his theory of hearing he postulated structures in the inner ear which would act as analyzers of the complex physical acoustic phenomena as they usually exist in the surrounding world. (Most sounds are physically "complex" only in the sense that they can be decomposed by special procedures into simple sinusoid vibrations; without such an artificial decomposition they form undivided, though not simple sinusoid vibrations; Hornbostel, 1926.) Sound analyzers of the cochlea have been identified with various non-nervous structures supporting sensitive hair cells of the papilla acustica basilaris. Most probably they are the elastic chords or strings composing the basilar membrane of the cochlea. (See Held, 1926.) By these the seemingly complex physical acoustic phenomena would be decomposed into their elementary or primitive constituents, into single, independent, simple sinusoid vibrations, corresponding with simple tones. These latter would by resonance cause a co-vibration of special groups of cochlear analyzers or strings, always the same for the same tone, and would thus stimulate certain, definite hair cells mounted upon the basilar membrane in the papilla acustica basilaris or the organ of Corti. In addition it can be said that Helmholtz' resonance theory of hearing implies an independent and separate transmission centralward, to the cerebral cortex, of definite independent stimulations intercepted by separate groups of hair cells. Each nervous current initiated by the stimulation of a given group of cochlear hair cells by using its own portion of the central auditory path would reach the auditory projection cortex without being deprived of its original, primitive form. It would be the task of the cortex itself to put together once more the elementary auditory neuro-biological phenomena into more complex cortical forms. From this angle, the function of the cochlear apparatus appears exclusively as one of analyzing or decomposing, the synthetic or integrative process in the audition being imagined as performed exclusively by the cortex.

Helmholtz' theory, attractive in its simplicity, though somewhat reshaped and adapted to modern requirements, has been most widely accepted and is at present the one most recognized, notwithstanding other numerous and quite different explanations.

Naturally many investigations have been undertaken to test or to reject Helmholtz' theory, among others, by the study of the nervous supply of the cochlea, especially of the organ of Corti. It has justly been assumed that if Helmholtz' theory, an eminently localistic explanation, is right, this would be manifested in a corresponding arrangement of neurons in the cochlea and in the higher links of the auditory path. The early investigators of the nervous supply of the cochlea, Retzius, Gehuchten, and Ramón y Cajal, indeed, found regularly arranged "radiated" nerve fibers terminating by small ramifications in the organ of Corti (compare also Ebner). Thus Helmholtz' theory appeared to have sufficient morphological support. But, other studies of Held (1897) and Kolmer (1924, 1926, 1927), including the recent studies of Held (1926) and Solovev (Solovtsoff), finding no "radiated" fibers or only a few, have apparently contradicted Helmholtz' conception.

Since Helmholtz' time many other hypotheses have been constructed (compare Waetzmann, 1926); some of them even endeavor to dispense entirely with the necessity of a decomposition of complex physical acoustic phenomena into primitive auditory sensations (Rutherford, 1898), or at any rate to place this decomposition in the central organ. All these various attempts, including that of Ewald (1899, 1922), can be said to completely disregard the character of the cochlear nervous supply, which, in view of the contradictory findings of the morphologists, was the line of least resistance (compare Bárány, 1928, and Börnstein, 1930).

However, as I endeavored to describe on another occasion in detail, the findings of modern investigators in regard to the nervous supply of the cochlea appear almost as a retrogression in comparison with the earlier results of Retzius, Gehuchten, and Ramón y Cajal. In my own previous studies of the character and mode of distribution of the nerve fibers in the cochlea (1927), I became convinced of the accuracy of the early observers who demonstrated the existence of isolated "individual" fibers arranged parallel to one another; this stands in good accord with Helmholtz' explanation of the nature of auditory processes. Moreover, other observations favor the acceptance of a stable projection of the cochlea upon the cerebral cortex though the

evidence is only indirect: the higher links of the central auditory path including the auditory radiation investigated in the present study, in so far as they convey auditory sensations to the cortex of the forebrain, bear, on the whole, the character of a "spatial" organization (although much detailed study remains to be done here; see my papers, 1926 and 1927).

At any rate, any theory of hearing which would favor a "diffuse" action of the auditory system, the latter working as a "whole," and would put the entire burden of sound analysis on the cerebral cortex (comparable to the purely "dynamic" concept of Gestalt psychologists), would unavoidably contradict the established morphological facts on the innervation of the inner ear, and would be difficult to reconcile with what we now believe to be some innate properties of the neuroplasm. (The total number of single, individual stimuli which can be transmitted by a motor nerve in a given time unit is limited by the duration of the refractory period, besides other factors, and does not, according to Lillie, exceed 500 in a second. No reasons exist to suppose a different action in auditory neurons.)¹ Since no "figures" are imaginable in a conducting system wholly homogeneously organized, the only way to explain the minute processes in hearing appears, therefore, to be to accept a kind of structural and functional differentiation of the whole auditory system into portions of unequal functional significance, as postulated by the theory of Helmholtz.

The morphological data on the nervous supply of the cochlea in my previous studies exceed, however, the requirements of Helmholtz' theory. These concern especially the course of the external spiral fibers of the papilla basilaris (see my paper, 1927; cf. especially Tello, 1931). It is evident that these must have some special significance for the act of hearing. This and other characteristics of the auditory system, which speak in favor of a regular "spatial" arrangement of the neurons conducting auditory impulses toward the cortex of the forebrain,

¹ Gildemeister (p. 302) came to a similar conclusion with respect to the acoustic nerve. Wever and Bray, however, found in their recent experiments on action currents of the auditory nerve of the cat, a frequency as high as 4100 per second. According to them the auditory nerve is an exception from all other nerves. Before being regarded as conclusive, these experiments which contradict all previous experiences and seemingly substantiate the "telephone theory of hearing" advanced by Rutherford and similar theories, must be tested for possible sources of error other than those already considered by the authors themselves. These may be changes of the potential in the inner ear owing to the vibrations of the endo-perilymph together with those of the membrana basilaris and membrana tectoria, changes occurring only as long as the normal conditions are maintained and ceasing soon after the death of the animal. (Compare also Adrian, *Jour. Physiol.*, vol. 71; and Davis and Saul.)

induced me to search for a more detailed explanation of the function of the structures of the entire auditory system, an explanation which might serve at least as a working hypothesis for future investigations. (It is not my intention to enter here into the discussion of the purely psycho-physiological aspect of audition in so far as this cannot be brought into direct connection with the anatomical structures.)

The sensory cells of the mammalian cochlea, the so-called hair cells of the papilla basilaris, are arranged in several outer rows of somewhat smaller, and one single inner row of somewhat larger elements (see Kolmer, 1924, 1927; Held, 1926). In the present consideration, unfortunately, these latter must be omitted since their innervation is insufficiently known. The outer rows of the hair cells representing the majority of the sensory acoustic elements form, in reality, a continuous receptor organ which is nothing else than a flat narrow spiral receptor surface stretching along the entire cochlea. This receptor organ, although it appears continuous, is not "diffusely" innervated. The nerve fibers which ramify with their telodendria around the outer hair cells, are of two kinds: "direct fibers" (orthoneura) and "spiral fibers" (spironeura) of Ebner. Both kinds of fibers unmistakably bear the character of "individual" neurons. That is, each single fiber ramifies around a limited number of sensory hair cells which form a well defined, close cell group, and does not come into contact with two or more such cell groups. Thus, each of either the "direct" or the "spiral fibers" receives impulses from a small number of closely neighboring hair cells and only from them. Some nerve fibers, however, touch one single hair cell only. But it can be assumed that the majority of cochlear nerve fibers actually terminate by small telodendria around a group of hair cells. Since in every simple, elementary auditory process (simple tone) not a single string or chord but several of these constituting the basilar membrane and forming a close isodynamic group of chords are put into vibration, not a single hair cell but a group of these mounted upon the vibrating group of basilar chords will be stimulated. It is, therefore, self-evident that not a single fiber but a group of closely neighboring cochlear nerve fibers will be used for the transmission centralward of impulses caused by every simple or elementary acoustic stimulus. Just as in the somato-sensory and in the visual systems, so also in the acoustic system, local signs or signatures are created since each hair-cell-orthoneural group is always stimulated by the same stimulus. Because the majority of fibers ramifying around the outer hair cells are "direct"

or "radiated" fibers (orthoneura) one appears justified in attributing to these the main rôle in the reception and transmission of acoustic excitations. They will represent the path for the main current of the auditory impulses centralward. The discrimination, that is, the distinction between two different elementary auditory sensations or tones, will very probably be based, in so far as the nervous structures are concerned, on the same structural principle of isolation as exists in the

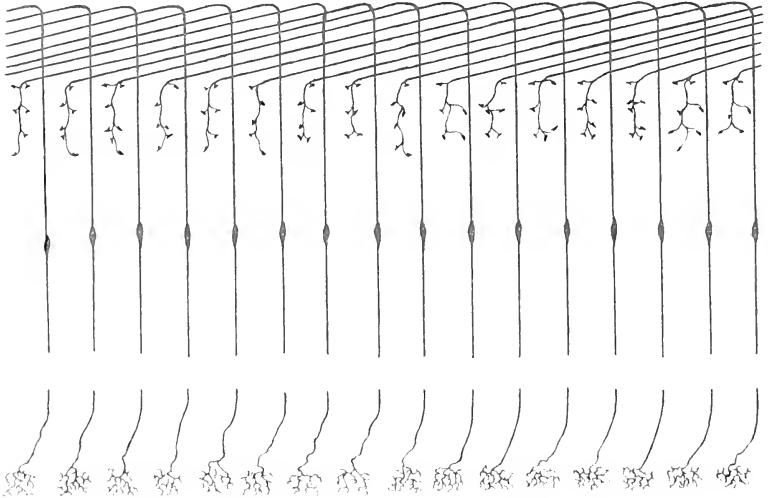


Fig. 11. A scheme to illustrate the internal organization of the central auditory path and its function. (For explanation see chapter XII.)

visual and somato-sensory systems. As described previously, a complete separation and isolation of the teledendra of auditory nerve fibers does not exist, for these latter partly overlap each other (exceptionally there are single terminating fibers). It appears plausible, therefore, that the purity of a simple acoustic sensation will depend on the complete separation of two correspondingly stimulated groups of hair cells, if, for instance, two pure tones are simultaneously perceived (in our scheme fig. 11, A_1 from A_2 , A_2 from A_3 , and so forth). In two such groups of hair cells the teledendra must not overlap. The

distinction between two simple stimuli will increase with the interval between two stimulated groups of hair cells. In such a way the discrimination, that is, the subjective distinction between two or more simple, elementary acoustic sensations, is achieved. In this respect the outer rows of hair cells together with their correlated groups of orthoneura (*A* system in our scheme) are comparable to the fovea and macula of the retina and to the macular portion of the visual path, although, because of partial overlapping of teledendra, the discriminating ability appears to be less in the auditory system than in the visual (since there does not exist an overlapping in the fovea centralis, compare: *Visual System* in the present treatise, and Ramón y Cajal, 1909-11, vol. 2, p. 347). This orthoneural apparatus of the inner ear must be looked upon as a highly discriminative acoustic receptor-conductor mechanism composed of a multitude of separate, minute receptor-conductor groups (since in each simple excitation only the corresponding receptor-conductor group is stimulated). This apparatus is, however, continuous throughout the entire cochlea and is, therefore, adapted for the reception of every primitive, simple acoustic stimulus or any combination of these, so far as these lie in the range of the octaves perceived by the human ear. The distinction and naming of the definite tones is, accordingly, a matter of conventional agreement. For, whatever the pitch of the initial or basic tone to which other subsequent tones in a series are referred, there always will be the same relation between the primary and secondary tones in a given formula.

So far as the perception and discrimination of simple tones and some of the more complex acoustic phenomena and so far as influence on pitch by intensity of stimulus is concerned, we have a relatively simple morphological explanation in the continuous and yet "spatially" organized orthoneural receptor and conductor system of the cochlea. More difficult to explain morphologically are the mutual relationships of several simple tones simultaneously perceived. These phenomena appear at present as conditioned by an unknown central, associative, or integrative cortical process. Can it be that certain interrelationships of several simple acoustic sensations called consonance, similarity of octaves, and so forth, can perhaps be brought into connection with certain morphological features of the nervous apparatus of the inner ear and be thus dispossessed of their mystical tinge?

It seems as if the external "spiral" fibers or spironeura, these also being "individual" neurons, with their regular arrangement and parallel turning in one direction, might help to explain the above phe-

nomena. An equal distance could be supposed for all spironeura (in our scheme fig. 11 the a system)—and there are some reasons to make such a supposition (see my paper, 1927)—which they have to pass from the group of hair cells where they terminate and where they receive impulses (for instance, for hair cell groups corresponding with the orthoneural groups A_1 , A_2 and so forth) along the outer rows of the hair cells to the point where they turn inward toward the spiral ganglion (for instance the spironeural group a_1 near the hair cell group corresponding with orthoneural group A_1). Further by supposing that their respective nerve cells belong to another segment of the spiral ganglion than do the nerve cells which send orthoneural fibers to the same group of hair cells, one would find a constant relation between the spironeural and orthoneural apparatus throughout the cochlea (A_1 to a_1 , A_2 to a_{II} , A_3 to a_{III} and so forth). If we now take the next step and accept the “spatial” organization of the entire central auditory path up to the auditory projection cortex, we would find each of the groups of hair cells maintaining a constant relation to two different groups of cortical cells (for instance hair cells A_1 to both cortical cell groups X_1 and X_{II} , A_2 to X_2 and X_{II} and so forth). According to that hypothesis there would exist from the cochlea to the cortex two different and yet intimately interrelated conductor systems: one corresponding to the orthoneural system (A) and the other to that of the spironeura (a), with constant relations between both. The result of such a double conductor system would be that whenever a single, definite group of hair cells is stimulated, that stimulus invariably finds its way centralward by two different groups of neurons (for instance by fibers A_1 , and a_1 , by A_2 and a_{II} and so forth) and would always reach two different groups of cortical cells (for instance, X_1 and X_{II} , X_2 and X_{II} and so forth).² Considering the small number of “spiral fibers” in comparison with the “direct fibers” one finds that the rôle of the spironeural apparatus (a -system) appears as complementary or accessory in respect to the main orthoneural apparatus (A -system) which transmits the main part of the nervous current underlying audition. This means that when a single group of hair cells, for instance those related to the orthoneural group of conductors A_1 , are stimulated, it will be the cortical group of cells X_1 which will receive the main stimulus, while the cortical group of cells X_{II} will get only a trace of such a stimulus (by the way of a_1 spironeura). The latter stimulus would in itself

² Compare Goebel, p. 114.

be insufficient to produce a definite sensation (in the present instance that of an octave), but will nevertheless suffice to create a certain functional correlation. When, therefore, at another time, two such correlated groups of hair cells are stimulated by two different stimuli, for instance A_1 and A_I , the previously created functional correlation will appear in subjective interpretation in the form of a "similarity" or a "resemblance" of these two stimuli. If on the contrary, two groups of hair cells which do not stand in connection by spironeural fibers are stimulated by two different simple stimuli (for instance A_1 and A_{II} , or A_1 and A_{III} , and so forth), no similarity in sensation will be evoked. It is pure supposition that the relation of an orthoneural and a spironeural group of neurons might amount to exactly one octave. Yet if this is proved by future investigations as true, the "similarity of octaves" will find its morphological explanation. (It is, however, possible that other relations co-exist with a smaller or a greater interval.) In this case the appearance of other phenomena called consonance (accords, harmonies) would be understood. A perfect consonance would exist between A_1 and A_I ; a pleasant impression would also exist between A_1 and A_{III} , A_1 and A_{IV} , A_1 and A_V , A_1 and A_{VI} since the distinction in perception must increase here (no uncertainty or indefiniteness as, for example, in relation of A_1 and A_{II} , the latter being close to A_I ; or between A_1 and A_{VII}). The phenomenon of dissonance can also be explained by the present hypothesis. A_1 is "dissonant" to A_2 (by reason of the immediate neighborhood). Since A_2 stands in a "consonant" relation with A_{II} , a similar "dissonant" effect will be produced if A_1 and A_{II} are stimulated simultaneously. The same explanation must be applied in respect to A_1 and A_{VII} since A_{VII} is in a "consonant" relation to A_7 , which in turn, is in a "dissonant" relation to A_1 . The subjective interpretation of the quality of similarity, of the degree of consonance or dissonance of any two tones will, therefore, depend on the interval or distance of two or more stimulated groups of hair cells from one another and on their spironeural connections; closely neighboring groups, when their orthoneural dendrites do not overlap, produce a sensation of two different tones, not pleasant when heard together, and equally so, if two groups of hair cells are stimulated which are close to the group which is by means of spiral fibers in the relation of an octave to one of the stimulated groups. Since for every group of hair cells throughout the cochlea there is another group which is in the relation of an octave to it—as many groups as there are octaves (A_1 to A_I , A_I to A_1 in circle,

and so forth)—hence there will be as many consonances and dissonances. With the help of the above scheme it is easy to construe any combination of two, or three, or more, harmonious or disharmonious, individual, simple stimuli in one or in several octaves. But the pleasant or unpleasant impression will always depend on whether, in such a combination, the stimulated groups of cells will be separated from, or will be next to, or near the groups of hair cells which by means of spironeural fibers are in the relation of octaves.

The hypothesis as to the minute function of the auditory mechanisms expounded above, goes further than to accept merely the decomposition in the inner ear of complex physical acoustic phenomena into primitive or elementary forms as postulated by the resonance theory of Helmholtz. The new point of view lays stress in greater degree upon the peripheral apparatus, even as regards the synthetic side of the auditory process. Already in the cochlea, according to this concept, certain definite and stable relationships of certain, definite, primitive, auditory processes would be achieved and would be transmitted to the cortex in a ready-made and more complex form. From this viewpoint the performance of the basilar membrane, with the orthon neural receptors-conductors *alone*, appears as that of an analyzer and a decomposer of complex sounds, while the rôle of the orthon neural and spironeural apparatus *taken together* is essentially that of a synthesizer. By explaining auditory processes in this way, the analysis appears greatly, perhaps entirely, as a peripheral process, yet at least a part of the synthesis also is accomplished in the peripheral organ. Such an explanation gives new meaning to the analyzing ability of the cochlea which, if existing alone, would be puzzling in view of the fact that the elementary forms of auditory sensations are undoubtedly put together again somewhere in the central organ, according to accepted opinion. From this new viewpoint, while it is true that elementary acoustic sensations are fused in higher centers, it is also true that, partly at least, the fusion takes place in the peripheral organ itself. Thus auditory sensations reach the cortex not as simple sensations, but as preformed complexes of elementary sensations, due to this peculiar double pattern of the cochlear nervous supply. The cochlear mechanism thus relieves the auditory cortex of part of its synthesizing functions and frees it for the truly higher mnemonic, integrating, ekphoric, and the like auditory processes which underlie the identifying of simple tones and related processes.

CHAPTER XIII

RESULTS OF THE PRESENT INVESTIGATIONS OF THE
AUDITORY SYSTEM

1. AUDITORY RADIATION

The uppermost link of the central auditory path, the internal geniculo-cortical or auditory radiation (*ar* in the corresponding figures), originates from the internal geniculate body. So far no evidence exists that a portion of the auditory radiation might originate elsewhere in the between-brain. This fiber system forms a thin, well defined fiber lamina comparable to a "fan" with its narrow "handle" placed near the internal geniculate body, and its broad wing expanding toward the cortex. The auditory fiber sheet or lamina is continuous, being interrupted only at the spot where its bundles divide to slip through the gaps between the islets of the ventro-caudal putamen. At first closely accompanying ventral bundles of the thalamo-cortical radiation (the latter emerging from the ventro-lateral nucleus of the thalamus), the auditory radiation enters the most ventral portion of the internal capsule, there forming a dense sheet of oblique fiber sectors immediately above the external geniculate body. Although close together near their origin, the auditory and the visual pathways do not mingle with each other appreciably. The auditory radiation crosses above and somewhat in front of the visual radiation where the latter forms the triangular field or zone of Wernicke. The course of the auditory path further laterally is partly between the islets of the ventro-caudal brim of the putamen and partly caudad to it. Lateral to the putamen, the auditory fibers fit at first into the stratum sagittale of the temporal lobe, forming that portion of it close beneath the claustrum, and then turn gradually toward the cortex, fascicle after fascicle. At first the most dorsal bundles turn; these are at the same time the most caudal; they enter the cortex in the posterior corner of the Sylvian fossa. The subsequent ventral bundles of the auditory sagittal stratum gradually deviate toward the more oral segments of the auditory projection cortex. The most ventral bundles enter the most oral segments of the auditory cortex. This indicates not only a regular or "spatial" arrangement of individual bundles of the auditory radiation but a similar organization of the auditory projection cortex as

well, segment alongside segment. The entire auditory radiation enters the white matter of the superior temporal convolution, and only that convolution. Here the auditory fibers occupy exclusively the upper half of the white matter close to the cortex lining the floor of the Sylvian fossa, leaving free the ventral third or half of the white matter along the cortex of the superior temporal sulcus (as do the visual fibers along the striate cortex; see Visual System). Some of the auditory fibers penetrate through the ventral "spur" of the claustrum and enter the capsula extrema to reach the cortex of the ventral wall of the Sylvian fossa. The arrangement of the auditory fibers in the white matter of the superior temporal convolution is remarkably regular, sectors of parallel fibers forming a thin fiber sheet. The entire auditory radiation enters the cortex of the upper lip of the first temporal convolution, in other words, the ventral wall of the Sylvian fossa. Only a few fibers reach the convexity of the superior temporal convolution on the free face of the temporal lobe. Neither the ventral wall of that convolution nor any other portion of the temporal cortex (middle, inferior temporal convolution) receives fibers of the auditory radiation, or any other afferent fibers from the subcortical nuclei.

No portion of the auditory radiation has been found to cross to the opposite hemisphere through the corpus callosum. (Compare Somatic Sensory System and Visual System.) The semidecussation of the central auditory path is achieved at lower levels of the neuraxis, principally in the medula oblongata and in the pons. (See my papers, 1925 and 1927.)

2. BOUNDARIES OF THE AUDITORY PROJECTION CORTEX. INTERNAL ORGANIZATION, FUNCTION, AND DISTURBANCES OF THE AUDITORY RADIATION AND OF THE AUDITORY PROJECTION CORTEX

According to the results here reported, the auditory projection cortex (deeply shaded area *a* in figs. 10 and 24) is a fairly well delimited portion of the temporal cortex, though its boundaries do not seem to be as sharp as those of the visual cortex. In this respect the auditory projection cortex resembles the somato-sensory cortex. The greater portion of the auditory projection cortex is buried in the Sylvian fossa, a small portion only emerging on the free face of the superior temporal convolution. The greatest number of the auditory fibers enter a small zone in the posterior corner of the Sylvian fossa, where

in the brain of the monkey an elevation of the cortex comparable with the transverse temporal convolution of Heschl of human anatomy can also usually be seen. This most richly supplied zone represents the "nuclear or focal zone" of the entire auditory projection cortex. According to this finding, the entire area 22 of Brodmann in the brain of the monkey (compare with fig. 7) does not belong to the auditory projection cortex but, at most, to only a portion of it. The remaining and larger portion of area 22, as well as the entire areas 20 and 21 of Brodmann, do not receive direct auditory or any other afferent fibers from subcortical regions and must be regarded as cortical centers of a higher order. However, all evidence speaks in favor of a more extensive cortical projection area of the cochlea than a narrow strip covering the transverse convolution of Heschl or even a part of it.

Besides the cortical area in the Sylvian fossa which undoubtedly belongs to the auditory sphere (area *a* in fig. 10), it was found in one of the experiments with an exceptionally large subcortical injury, that the cortex along the posterior extremity of the Sylvian fissure as far back as the vicinity of the simian fissure also receives afferent fibers from the between-brain (area *x* in fig. 10). However, it was not possible to determine whether that posterior Sylvian receptive area also belongs to the auditory projection cortex and is, perhaps, its caudal continuation; or whether it represents a special projection area of an unknown significance. (In Minkowski's [1923] Experiment 4 the antero-dorso-median portion of the internal geniculate body, besides the pulvinar and the dorso-lateral thalamic nucleus, degenerated after the ablation of Brodmann's areas 5, 7, and the neighboring portion of area 22; see also his Experiment 5.) That latter receptive area is also for the greater part hidden in the Sylvian fissure and receives abundant afferent fibers of large caliber.

Since there exists a single auditory radiation terminating in a single cortical projection area of fairly small size, it is permissible to conclude that all auditory impulses, in so far as they reach the cerebral cortex, must first pass that afferent path and its terminal cortex, which is the auditory "gateway" of the entire hemisphere, no matter what the special nature or quality of the auditory impulses may be. Only from that region are the auditory impulses further distributed to the surrounding cortex of the temporal, insular, and parieto-occipital lobes, the latter regions being the seat of "higher" auditory and associated processes. The question of what fiber systems mediate this further process of distribution and diffusion of incoming auditory

impulses must be settled by further investigations. At any rate, the assumption that a large portion of the temporal lobe, or perhaps that entire lobe, receives direct auditory impulses from the subcortical regions has little anatomical evidence to support it. (In the present studies the hippocampal and cingular convolutions and their possible afferent paths were not considered.)

To the question of the internal organization of the auditory radiation these studies can give only a general answer. However, the present observation that the internal geniculo-cortical radiation forms a thin fiber sheet or lamina composed of regularly or "spatially" arranged, parallel fibers and fiber bundles, each terminating in a different segment of the auditory projection cortex, together with other evidence collected previously (see my papers, 1925, 1926, 1927), corroborates the view of a fixed or stable projection of the auditory peripheral receptive surface (papilla basilaris of the cochlea) upon the cerebral cortex.

Since the uppermost link of the central auditory path is a definite anatomical and functional entity confined to a comparatively narrow space in the hemisphere and since it terminates in a definite circumscribed area of the temporal cortex, we are permitted to conclude that the entire auditory radiation can easily be interrupted by a single subcortical lesion. This will more readily occur when the seat of the lesion is close to the origin of the auditory radiation where all its fibers are assembled into one bundle ("handle" of the fiber "fan" of the radiation), while nearer the cortex small lesions will be likely to interrupt only a portion or portions of the radiation and thus produce one or several gaps in tone perception comparable to scotomata of the visual fields. A similar partial loss of the auditory function can be expected from small injuries to the auditory projection cortex because of the unequal functional significance of different segments of that area.

PART III
VISUAL SYSTEM

CHAPTER XIV

ORIGIN, COURSE, AND TERMINATION OF THE VISUAL RADIATION. LOCATION AND EXTENT OF THE VISUAL PROJECTION CORTEX. PROJECTION OF THE LATERAL GENICULATE BODY UPON THE STRIATE AREA (FINDINGS)

In five of the experiments reported here (Experiments I, II, III, IV, and V-A) the visual radiation was partly interrupted. The interruption was made either at the origin of the visual fibers in the external geniculate body or close to it. In each of these experiments the interrupted portion of the radiation degenerated toward the occipital lobe and was traced in successive sections of the continuous five series, stained according to Marchi's method, to its respective cortical termination. The purpose of such a study was not only to determine the general course and termination of the visual radiation but also to analyze its constituent bundles—their mutual or relative position, their course, and especially the relation of each of these bundles to its special origin in the external geniculate body on the one hand, and to its special segment of the visual cortex on the other. Since the seat of the injury in each of the five experiments was somewhat different, the bundles degenerated in each case were only partly identical. By comparing all bundles or segments degenerated in all five experiments one with another and by checking up the results of the present investigations with those obtained previously by Brouwer and Zeeman, an attempt has been made to reach a properly supported conclusion as to the organization and function of the entire afferent visual path.

In addition to this five other experiments are reported here where either small portions of the striate area (alone or with a portion of the visual radiation) were damaged (Experiment V-B and V-C); or where the striate area was almost or entirely removed (Experiment V-D and V-E). In these experiments the purpose was to study the retrograde cell degeneration of the lateral geniculate body according to Nissl's method and in particular (*a*) to correlate the number, the size, and the position of small degenerated zones in the lateral geniculate body with the number, the size, and the position of the lesions

in the striate area; thus it was hoped to obtain an insight into the projection of various segments of the lateral geniculate body upon the striate area on the one hand, and to prove or to disprove the existence of an anatomical basis for the preservation of "figures" in the visual acts on the other hand; and (b) to prove or disprove the existence of the crossed connections between the lateral geniculate body and the striate area ("Fasciculus corporis callosi cruciatus," and the like); to verify the existence of other side-paths of the visual radiation, and the existence of the so-called "intercalated neurons" ("Schaltzellen" of Monakow) within the lateral geniculate body, and also the existence of a projection of the superior colliculi of the midbrain upon the cerebral cortex, and the like problems.

EXPERIMENT I

By the lesion in this experiment (*L* in figs. 36, 37), described previously (see Chapter V), two bundles of the external geniculo-cortical radiation were interrupted (vr_1 and vr_2 in figs. 37-41). They constitute the intermediate segment or the perpendicular branch of the parieto-occipital sagittal strata. The dorso-ventral extent of each bundle is about one millimeter, with an intermediate zone of about one millimeter between both bundles left unaltered. Both these compact degenerated bundles were followed up to the visual cortex. However, besides these two fairly distinct bundles well separated from each other, a considerable number of degenerated visual fibers were seen scattered among the normal fibers of portions of the sagittal strata not injured directly. Many of these were found in the vertical branch of the strata (*rvert* in fig. 39), and a few in the dorsal horizontal branch (*rhs*) while the ventral horizontal branch remained almost free (*rhi*). This somewhat diffuse degeneration was due, it must be assumed, to a slight alteration of the internal and the intermediate segment of the external geniculate body caused by the neighboring lesion of the diencephalon, and to the direct slight injury of the posterior spur of the external geniculate body (figs. 34 and 35), whereas the external segment of the external geniculate body being more distant, remained unaltered. Thus, it is the middle or the perpendicular (vertical) branch of the external sagittal strata which degenerated in this experiment. Callosal fibers from and to the occipital lobe, being more dorsally situated, on the whole, escaped the injury. These as well as the efferent and the association fibers were neglected.

Of particular interest was the study of the course and termination of both compact degenerated bundles. At their beginning near the lesion and immediately caudad to it, both bundles are composed exclusively of degenerated fibers (figs. 37, 38) and contain fibers of a different caliber: fairly coarse and finer fibers. While all the coarser fibers were traced toward the visual cortex, a number of finer fibers soon disappeared farther caudad thus revealing their different origin, course, and significance.

The two compact degenerated bundles have approximately a rhomboid and later a trapezoid shape, and occupy exclusively the external sagittal stratum of the parieto-occipital lobes. This was especially evident after a number of finer degenerated non-visual fibers had disappeared. Yet even farther caudal, the number of fine fibers exceeds that of the coarse, the latter representing only a minority of all fibers composing the external sagittal stratum.

On the whole, the afferent visual fibers, irrespective of their caliber, preserve during their course occipitalward their position within the external sagittal layer leaving the narrow internal sagittal layer and, of course, the tapetum entirely free.

Both compact degenerated bundles (vr_1 and vr_2) preserve their relative position to each other as far caudad as the occipital lobe and can be distinguished as separate individual bundles (figs. 38-41). Later on when they approach the striate cortex marked by the dotted intracortical stripe in corresponding figures of sections through the occipital lobe, showing the striate area in its full extent, both bundles gradually merge (fig. 42). This apparent mixing of fibers formerly belonging to separate bundles, apparent only on a superficial examination, is the consequence of the considerably changed topographic conditions in the white matter of the occipital lobe. The fibers, namely, when they reach the occipital lobe, change from a longitudinal-sagittal direction into an ascending course or turn gradually laterally or medially to reach their special segments of the striate area. As a matter of fact, even in the occipital lobe near their termination the two separate degenerated zones are fairly well discernible, and their fibers can be traced individually to different portions of the striate area.

It was of interest to notice that no degenerated fibers of the sagittal strata, be they coarse or fine, either from the two separate bundles or from scattered degenerated fibers turn toward the cortex of the parieto-occipital lobe except when they approach the striate area. Before they enter the striate cortex they form laterally to the external

sagittal stratum the so-called stratum extremum of R. A. Pfeifer (1925). Both the coarse and fine fibers finally reach the cortex of the occipital lobe which is distinguished by the presence of the stria Gennari or Vieq d'Azyr.

First the ventral compact bundle turns toward the striate cortex (vr_2 in figs. 40, 41). It enters the ventral half of the striate area below the shallow oblique sulcus calcarinus externus (Sos visible in figs. 42, 43, as a sharp indentation in the right side of figures), on the external face of the occipital lobe called the operculum occipitale. A little farther caudal the dorsal bundle begins gradually to ascend dorsalward (vr_1 in figs. 41-43); it gives off its fibers to the dorsal portion of the operculum occipitale above the sulcus calcarinus externus, to the dorsal margin of the occipital lobe, and, together with the numerous scattered degenerated fibers of the remaining portion of the perpendicular branch of the external sagittal layer, it supplies the pole of the occipital lobe. The few scattered degenerated fibers of the dorsal horizontal branch gradually turn medially toward the upper lip of the calcarine fissure. Accordingly, the ventral compact, degenerated bundle of the present experiment supplies the ventral and somewhat more anterior half of the visual cortex on the external face of the occipital operculum near the ventral extremity of the sulcus simialis and between the sulcus calcarinus externus (Sos) and the inferior occipital sulcus. The dorsal compact bundle supplies the dorsal and somewhat more posterior half of the same occipital operculum and both the external and internal face of the occipital pole (fig. 1; compare also Experiments II, III, IV, and V-A). In other words, the intermediate perpendicular branch of the visual radiation supplies the striate area covering the external face of the occipital lobe as well as the occipital pole, while the dorsal horizontal branch of the radiation supplies the striate area of the upper lip of the calcarine fissure. (The ventral horizontal branch, which in this experiment remains normal, supplies, accordingly, the ventral lip of the fissura calcarina.)

From the study of the finer details of the course of the degenerated visual fibers, other important conclusions can be deduced. First, the afferent visual fibers arranged in a parallel fashion are distributed in a remarkably uniform and regular way over the corresponding segment of the striate cortex. (Compare, for example, fibers of the ventral bundle streaming toward the cortex in fig. 41, and the dorsal bundle near the dorsal margin of the lobe in fig. 42.) Each of the segments of

the striate cortex, supplied by compact bundles, receives everywhere numerous afferent fibers. There do not exist, accordingly, any small portions of the visual cortex without an adequate afferent fiber supply, or any gaps in that supply, so far as can be determined by the method applied here. (Compare identical observation with regard to the supply of the somatic sensory cortex around the sulcus centralis, Chapter VII.) Where the compact degenerated bundles enter the cortex their fibers tend toward it in a uniformly arranged stream. Attention must also be called to the particularly dense fiber supply of the external, opercular portion of the striate area, especially around the shallow sulcus calcarinus externus (sulcus occipitalis superior), and of the entire occipital pole (for explanation see Chapter XVI and XVII).

The further observation is that all afferent visual fibers, degenerated in this experiment, enter the striate area exclusively. It is striking to see how strictly these fibers observe the limits of the striate cortex. When still in the subcortical white substance the fibers keep close to that side where the stria of Gennari or Vieq d'Azyr is visible, leaving the remaining portion of the white substance free (lower part of figs. 40-42; a similar feature was observed in all four remaining experiments; see figs. 13, 56, 57, 72-76). On sections where both the striate and peri-parastriate cortex appear, degenerated afferent visual fibers enter exclusively that portion of the cortex which contains the stria Gennari corresponding with Brodmann's area 17. The boundary between the cortex receiving afferent visual fibers and the remaining cortex is in all sections as sharp as the limits of the stria Gennari or Vieq d'Azyr and is, in fact, identical with the latter (dotted stripe in the lateral portion of the striate area, right lower corner in figs. 40-43).

As to the extent of the visual cortex receiving afferent fibers in this experiment the following can be said: On the external face of the hemisphere the supplied portion of the cortex includes the entire striate area occupying almost the whole occipital operculum (shaded area in fig. 1, upper figure, compare with fig. 7, field 17). The boundaries of the supplied cortical area and those of the striate area or field 17 of Brodmann, are exactly congruent, as already mentioned. Other areas, fields 18 and 19 of Brodmann, surrounding the striate area (in front and behind the sulcus simialis *Ss*) remain entirely free of any degenerated fibers. On the medial face of the hemisphere the area striata also receives cortico-petal visual fibers although not in its entire extent (fig. 1, lower figure). Here the supplied segment includes

the entire pole of the occipital lobe caudad to both the ascending and descending branches of the calcarine fissure (*Fcalc*). A small number of fibers enter the upper lip of the calcarine fissure, corresponding to the small number of degenerated fibers in the dorsal horizontal branch of the external sagittal layer. They reach the latter region by gradually turning around the dorsal corner of the lateral ventricle downward where they form a thin fiber layer. This will be better demonstrated by Experiments II, III, and IV (figs. 55-57, 69-72, 75, 76). It was also noticed that in the calcar avis the visual fibers before entering the cortex run for a distance oralward. Also the fibers destined for the upper lip of the calcarine fissure are, in the present experiment, not everywhere equal in number nor uniformly distributed. (See different observation in other experiments.) This is due to the fact that, unlike what was observed in Experiments II, III, and IV, no compact bundle supplying the upper lip of the calcarine fissure (upper horizontal branch) was caused to degenerate in this experiment, but a few scattered fibers only. The relation between the afferent visual fibers and the striate cortex of the upper lip of the calcarine fissure is exactly the same as described for the occipital operculum. No afferent fibers whatsoever reach the extra-striate cortex. While on the other hand, the ventral lip of the calcarine fissure did not, in this experiment, receive any such fibers. This is due, as expected, to the fact that the ventral horizontal branch of the sagittal layers and the lateral segment of the external geniculate body remained unaltered in the present experiment. The most posterior portion of the calcarine fissure, its ascending branch, however, is reached by a great number of degenerated fibers.

The caliber of the afferent visual fibers is in general considerably below that of the somatic sensory and auditory fibers. (Compare Somatic Sensory System and Auditory System.) There are, as mentioned, some differences in size also among the visual fibers, the majority of these being fairly delicate. Also there are regional differences since the fibers supplying the occipital operculum are fine and of about equal caliber, a few of them only being coarse; whereas the coarser fibers enter the striate cortex lining the calcarine fissure. It was also noticed that individual bundles close to the external geniculate body are composed of fibers having an equal caliber, though there are differences in caliber in different bundles.

It must also be mentioned that, although in the present experiment a considerable portion of the entire external geniculo-cortical

radiation degenerated, no evidence was found of afferent fibers crossing through the corpus callosum to the opposite hemisphere. (See the same observation in the following experiments.)

EXPERIMENT II

In Experiment II, so far as the visual system is concerned, the lesion (*L*) is strictly limited to the internal segment of the external geniculate body (*Cgl*), close to the thalamus, as figure 51 clearly demonstrates. (For other details on the lesion see Chapter V and X.) The remaining and by far the larger portion of the external geniculate body, its intermediate and its external segments as well as the entire visual radiation including its beginning (Wernicke's triangular field), entirely escaped direct injury (figs. 52-57). Also no callosal, association, or any other fibers of the parietal and occipital lobes were damaged in this experiment.

From the sharply localized lesion of the external geniculate body, one single compact bundle of the visual radiation degenerated occipitalward; namely, that originating from the damaged inner and somewhat oral segment of the body. On well stained sections of our uninterrupted series it was possible to study the bundle in question from its origin, along its entire course, to its termination in a definite portion of the visual cortex (figs. 51-57, 65).

The origin of the degenerated bundle was clearly discernible. Fine bundles of degenerated fibers, all of about equal size and lying strictly parallel to each other, spring from the internal contour (these fibers being somewhat stronger) and from the dorsal margin of the external geniculate body (these fibers being somewhat thinner). At the beginning the degenerated fibers when passing the internal capsule necessarily mix with other fibers that remain normal (callosal, associational, efferent, and so forth), and also gradually change from an ascending to a sagittal direction (*vr* in fig. 52).

Some of the degenerated fascicles ascending from the damaged portion of the external geniculate body turn medially and dorsally close along the thalamus and pulvinar forming a narrow sickle-shaped bundle. Unfortunately it was impossible to ascertain whether these fine medial fibers belong to the cortico-petal visual path or whether they enter the thalamus, or pulvinar, or anterior colliculus. Thus the question of a possible connection between the external geniculate body

and the thalamus must be left open (either special neurons¹ or collaterals of incoming peripheral optic fibers or such collaterals given off by fibers of the visual radiation).

The degenerated cortico-petal visual fibers after leaving the triangular field of Wernicke and after crossing the internal capsule where they lie somewhat scattered (fig. 52, degenerated area *vr* above the external geniculate body) gradually gather and become condensed into one, single degenerated zone corresponding with the dorsal horizontal branch of the external sagittal stratum (*vr* in figs. 53-57). It is natural that the visual path while still in the internal capsule does not form a compact fiber system; the majority of capsular fibers belong to other fiber systems. Only when visual fibers reach anterior levels of the occipital lobe do they approach close enough to form a dense fiber sheet composed almost exclusively of visual fibers (figs. 55-57). Here these fibers occupy, consequently, a smaller territory. When the sagittal strata of the parieto-occipital lobe take their proper shape, the afferent visual fibers remain strictly within the limits of these fiber formations and remain so till they approach their cortical termination.

The bundle of the visual radiation springing from the internal segment of the external geniculate body forms, accordingly, the dorsal horizontal branch of the external sagittal layer (*vr* in fig. 55). This bundle represents the dorso-medial rib or radius of the fiber fan of the visual radiation. Its degenerated fibers, similarly as in Experiment III and also in Experiments I, II, and V-A, do not mix to any considerable extent with the postero-dorsal fascicles of the somatic sensory (thalamo-cortical) radiation (*sr* in figs. 52, 53; a prolonged confusion was produced when these thalamic fibers were proclaimed a portion of the visual system). The visual fibers, although close to and immediately below the somatic sensory fibers, occupy in reality a separate zone. Soon, however, both visual and somato-sensory fibers separate from each other. The degenerated zone of the visual portion of the parieto-occipital sagittal strata occupies from one-half to two-thirds or even three-quarters of the thickness of these layers which is the external sagittal stratum. Although the latter gradually decreases in size occipitalward, it becomes relatively larger as the internal stratum is reduced. Fibers of the degenerated visual bundle are

¹This does not appear probable because in the experiments of Brouwer and Heuven after destruction of the striate area, all the cells of the external geniculate body degenerated. The same is proved by our Experiment V-D and V-E. See these.)

fairly equally distributed to the whole degenerated zone, the latter being otherwise sharply delimited.

Farther occipitalward the degenerated bundle slowly ascends and at the same time gradually turns medially. Bending around the callosal bundle (tapetum) and above the dorsal corner of the lateral ventricle it finally reaches the upper lip of the calcarine fissure. Here the degenerated area has the shape of a thin twisted fiber lamina (figs. 55-57).

The afferent visual fibers, as mentioned above, remain strictly confined to the external sagittal layer during their entire course occipitalward leaving that layer only when approaching the striate cortex. After the most caudal somatic sensory fibers have left the sagittal strata, practically no degenerated fibers whatever deviate toward the cortex until the area striata, marked by a dotted stripe in the corresponding figures, appears. This point was studied with particular care in Experiment II as well as in the remaining experiments where special attention was paid to sections showing deep fissures closely approaching sagittal layers (for example, figs. 55-57, compare also figs. 13, 40, 41, 71, 72, 75, 76 in Experiments I, III, IV, and V-A). It appears justifiable, therefore, to maintain the dictum that visual fibers do not reach any cortical region which does not belong to the striate area or field 17 of Brodmann. So also, neither in this nor in any of the present experiments, have visual fibers been seen to turn into the corpus callosum in order to reach the opposite hemisphere in this way (figs. 52-54). The evidence was particularly clear in the present experiment, since no callosal fibers whatsoever degenerated.

Finally the degenerated visual fiber bundle gradually turns medially and enters the striate cortex of the upper lip of the fissura calcarina (figs. 55-57). The region supplied by that bundle is a well delimited one, corresponding with a long narrow strip of the striate cortex buried in the calcarine fissure (upper lip). As the present degenerated bundle represents the dorsal "boundary bundle" of the entire visual fiber fan, so the portion of the striate area supplied by it represents also a "boundary zone," the most dorso-medial, of the entire visual projection cortex (fig. 2, lower figure).

A few more details must be mentioned since they are apparently important for an understanding of the finer arrangement and cortical distribution of individual bundles composing the visual radiation. In sections where the most anterior portion of the striate cortex appears lining the bottom of the calcarine fissure, individual degenerated

fibers and small fascicles of these turn from the common bundle ventrally and again obliquely laterally along the inner contour of the lateral ventricle before they actually enter the cortex in the most anterior portion of the striate area where they just reach the floor of the fissure (figs. 55, 56). They must describe a turn of about two hundred and seventy degrees or more which they complete by a spiral course ascending first caudally, then turning medially around the posterior horn of the lateral ventricle, and descending toward the upper lip of the calcarine fissure. The ventral segment of the visual radiation must have a similar spiral course occipitalward, although in none of the present experiments was that portion of the radiation demonstrated by degeneration. It is this ventral visual bundle which forms the ventral horizontal branch of the external sagittal stratum (*rhi* in fig. 55), the latter, however, passing ventrally below the posterior horn on its way to the lower lip of the fissura calcarina (as a few solitary degenerated fibers demonstrate). The remaining intermediate bundles of the visual radiation composing the vertical (perpendicular) branch of the external sagittal layer (*rvert* in fig. 55), for example, the two compact bundles degenerated in Experiment I, and the bundle M in fig. 13 of the Experiment V-A, have a more direct longitudinal course toward the operculum occipitale and the occipital pole, as described in the preceding experiment, and as it will be described later.

Within the upper lip of the calcarine fissure, in the present experiment, the visual fibers enter the cortex medially toward the edge of the lip only as far as the stripe of Gennari or Vicq d'Azyr is visible. The limit between the supplied and unsupplied cortex corresponds here, as in other experiments where a "boundary segment" of the visual radiation degenerated, exactly to the limit of the striate cortex (figs. 55-57, 65).

Since the degenerated bundle represents a comparatively small portion of the entire visual radiation—sufficiently and clearly demonstrated by the fact that in the present experiment the perpendicular and ventral horizontal branch of the external sagittal layer remained normal—it was not unexpected to find that the portion of the striate area supplied by degenerated fibers was also a narrow strip. This strip stretches along the entire calcarine fissure from its oral beginning (where the striate area appears) as far caudalward as the upper end of the ascending branch of the calcarine fissure (in front of the latter branch). The narrow shaded area in figure 2, along the horizontal portion of the calcarine fissure (*Fcalc*), indicates here, as in

other experiments, only the longitudinal extent of the supplied cortex, since in the monkey the striate cortex does not reach the convex face of the lips of the fissure except along both ascending and descending branches. Of particular interest is the fact that the narrow oblong strip of cortex supplied by the degenerated bundle at its oral beginning where the striate area appears in the bottom of the fissura calcarina, represents also a narrow zone (dorsal half of the narrow striate area) and increases in extent farther caudad toward the occipital pole in the same way as the striate area extends toward the edge of the upper lip. The shape of the supplied segment of the striate area, accordingly, resembles that of a narrow triangle with its sharp point at the anterior beginning of the calcarine striate cortex, its wider end turned occipitalward.

From the above description it is clear that a small segment of the external geniculate body, in the present experiment the internal segment, gives origin to a number of central visual fibers which form during almost their entire course a well delimited, compact bundle with a definite course and position (except during its passage through the internal capsule where its fibers lie somewhat scattered), which bundle supplies a small, well defined, triangular segment of the area striata, here a "boundary zone" of the upper lip of the fissura calcarina. No other cortical region of the striata area (lower lip, external face of the occipital opercle, occipital pole) or of the peri-parastriate area (areas 18 and 19 of Brodmann) stands in connection with the inner segment of the external geniculate body. The supplied cortical triangle stretches along the entire upper lip of the calcarine fissure, as far as the latter contains the striate cortex, and is slightly twisted spirally around the axis of the fissure. The fiber supply of the triangular cortical segment is everywhere about equally abundant and uninterrupted, nowhere showing gaps. (Compare Experiment I.) On numerous well stained sections dense bundles of degenerated fibers approach the upper lip of the fissure to enter finally the striate cortex (fig. 57, 65).

These features regarding the origin, course, and termination of the single fiber bundle degenerated in this experiment when taken with facts established in the four remaining experiments corroborate the view that the individual fibers of the visual radiation which take origin in closely neighboring portions of the external geniculate body, form compact bundles and enter closely neighboring portions of the visual cortex (this meaning the "neighboring" or "spatial" arrangement of fiber fascicles of the visual radiation). (See Chapter XIX.)

EXPERIMENT III

In this experiment by a direct lesion of the visual radiation while still in the internal capsule, at the level corresponding with figure 52 of Experiment II, an almost identical portion of the radiation as in Experiment II, and partly corresponding with the degenerated segments in Experiments I and IV (namely with those supplying the dorsal lip of the calcarine fissure) was caused to degenerate and was traced up to its termination in the visual cortex (*vr* in figs. 66-74). This bundle represents here, as well as in Experiment II, the dorsal rib or radius of the whole visual radiation, appearing on all sections through the parieto-occipital lobe as the dorsal horizontal branch of the external sagittal stratum. The number of degenerated fibers in the present experiment must be almost equal to that in the foregoing experiment since the degenerated area of the external sagittal layer has about the same extent and position. (Compare figs. 69 and 71 with fig. 55.)

The course, position, and termination of the single degenerated bundle is in all details the same as in Experiment II. The caliber of its fibers is fairly coarse and also of medium size; yet the visual fibers do not attain the caliber of the coarse somatic sensory fibers. The latter (*sr* in the figs.) accompany the degenerated visual bundle on its dorsal side to a longitudinal distance of about one centimeter and turn toward the dorsal segments of the postcentral and superior parietal convolution (*PS* in figs. 69, 71); whereas the degenerated visual fiber bundle proceeds occipitalward (a few callosal and other fibers degenerated in the present experiment will be neglected; they can easily be distinguished from the proper visual bundle by their position in the tapetum). The visual bundle in question degenerated almost completely. It formed in all sections a sharply defined area close to the lateral margin of the sagittal layers. The degenerated area or its fibers do not appreciably mingle with the bundles remaining normal. (Compare especially fig. 72). This is especially evident in sections through the occipital lobe where both the internal sagittal stratum and the tapetum, as well as the entire remaining white substance of the hemisphere laterally from the external sagittal layer, remain completely free from degenerations.

On levels behind the splenium of the corpus callosum as soon as the calcarine fissure takes its proper shape, the degenerated visual fiber

bundle changes its position (figs. 69, 70). From then on occipitalward it occupies the dorsal horizontal branch of the external sagittal layer corresponding with the upper lip of the calcarine fissure. Its fibers in their course occipitalward gradually shift medially and soon, in sections showing the oral segment of the striate cortex lining the bottom of the fissura calcarina, begin to descend ventrally by bending around the hook-shaped bundle of the callosal fibers (tapetum, *Tap* in fig. 70) near the dorsal corner of the lateral ventricle, and penetrate as individual fibers and as thin fascicles of these into the upper lip of the calcarine fissure (in figs. 69 and 70 the small branch of the common degenerated bundle directed medially and pointing toward the edge of the upper lip does not actually enter the cortex here, but on more caudal sections where the striate cortex extends more medially; see figs. 71, 72). Since the oral segments of the striate cortex are confined to the bottom of the calcarine fissure, the individual visual fibers and bundles of these have to describe a spiral turn of scarcely less than three hundred and sixty degrees before they can reach the striate cortex (see Experiment II). Farther up caudad the striate cortex gradually extends more medially toward the inner face of the hemisphere, approaching but not quite reaching the edge of the upper lip of the calcarine fissure (see figs. 71-73, and lower degenerated bundle in fig. 74). In the same way the degenerated visual fibers shift medially with the changing boundary of the striate cortex. Yet the incoming afferent visual fibers never overstep that boundary. To demonstrate the strict congruence of the boundaries of both the striate cortex and the cortical segment receiving degenerated visual fibers in the present experiment, two illustrations have been prepared of the dorsal lip of the fissura calcarina of figure 71 under a higher magnification clearly illustrating the actual conditions (figs. 72, 73; the latter figure is turned almost ninety degrees in comparison with figs. 71, 72). The striate cortex is indicated here by the presence of a double or a triple horizontal intracortical stripe, the closest to the surface of the cortex being the stria Gennari or *Vieq d'Azyr*. The striate cortex, as can be seen, ceases quite abruptly at the points indicated by the arrow. In the same way the entering cortico-petal visual fibers, black lines and dots in the figures, stop at the limit of the stripes. A similar strict observance of the boundaries of the striate cortex by the afferent visual fibers exists in the entire present series as well as in the remaining series whenever a "boundary bundle" degenerated (compare especially fig. 76 in Experiment IV). No visual fibers whatever enter

the cortex bordering the striate area belonging to the area periparietaria of Elliot Smith or fields 18 and 19 of Brodmann. The same was observed in sections where the striate cortex extends upon the free face of the hemisphere along the ascending branch of the calcarine fissure *Fc* (upper degenerated bundle in fig. 74, see also lower figure in fig. 3 and compare it with fig. 7). The boundary of the cortical segment which in this experiment receives afferent visual fibers and the medial boundary of the striate area of the upper lip of the fissura calcarina are consequently congruent and identical. Figures 69, 71-74 also demonstrate the course of the degenerated visual fiber bundle which while still in the white substance keeps close to the striate cortex, leaving the remaining portion of the white substance along the non-striate cortex entirely free.

The shape of the segment of the striate cortex supplied in the present experiment by the fibers of the single degenerated bundle of the visual radiation resembles that of a narrow triangle stretching along the upper lip of the main undivided horizontal branch of the fissura calcarina (*Fcalc*) and in the anterior lip of the ascending branch of that fissure (lower figure in fig. 3, shaded area; compare with fig. 7). This cortical segment, as could be expected, is identical with a similar segment delimited in Experiment II (lower figure in fig. 2). In Experiment III, as in other experiments, the shaded area in figure 3 along the main horizontal branch of the fissura calcarina indicates merely the longitudinal extent of the supplied cortical segment, this segment emerging on the free internal face of the hemisphere only along the ascending branch of the fissure.

Finally special emphasis must be laid upon the fact that no degenerated visual fibers were seen, in the present experiment, to reach any portion of the parieto-occipital cortical region covering the inner and outer face of the hemisphere which does not belong to the striate cortex. But likewise no degenerated fibers enter any other portion of the striate area itself (lower lip of the calcarine fissure, occipital operculum, occipital pole) except the described segment in the upper lip and in front of the ascending branch of the calcarine fissure. Also no visual fibers were seen entering the corpus callosum in order to reach the opposite hemisphere.

EXPERIMENT IV

In this experiment in a similar way as in Experiments II and III, one single bundle or segment of the visual radiation was interrupted by a lesion in the parietal lobe. The instrument, a small Graefe's knife, was plunged about two centimeters into the hemisphere through

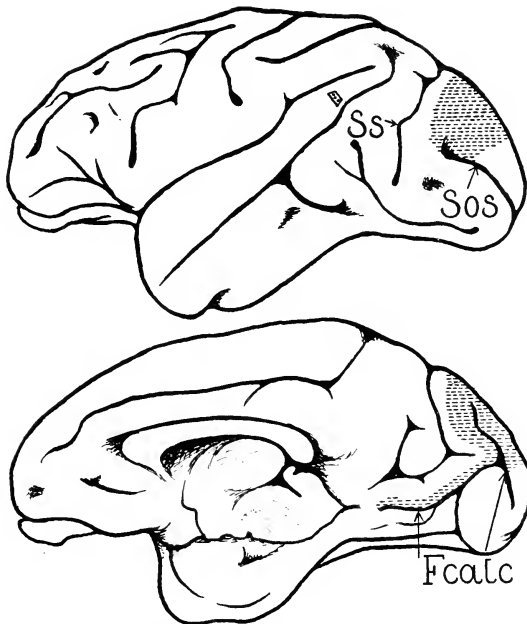


Fig. 12, Experiment IV. External (upper figure) and internal (lower figure) face of the monkey's hemisphere showing the location and extent of the visual projection area of the cerebral cortex found in this experiment (shaded area). The visual area occupies the larger anterior portion of the upper half of the occipital operculum behind the simian sulcus (*Ss*) and above the external calcarine sulcus (*Sos*) over the lateral face of the hemisphere. Over the medial face it stretches along the upper lip of the horizontal branch of the calcarine fissure (*Fcalc*) and over the upper half of the occipital pole along the ascending branch of the fissure. Small dotted area in the posterior portion of the superior temporal convolution represents the superficial lesion through which the knife was introduced into the substance of the hemisphere. (Compare figs. 75, 76.)

the convexity of the posterior portion of the superior temporal convolution, as figure 12 shows (small coarsely dotted area). The bundle of the external sagittal stratum interrupted in such a way is about

equal in size to the individual degenerated bundles in other of the present experiments (Experiments II and III). It is situated at the limit between the dorsal and the middle third of the vertical branch of the sagittal strata on levels where the latter attain their usual shape (parietal lobe). It accordingly corresponds to a fiber segment immediately ventral to that degenerated in Experiment II (fig. 54) and in Experiment III (fig. 68), or approximately to the upper degenerated bundle in Experiment I (figs. 38 and 39) though it extends somewhat toward upper horizontal branch.

The degenerated zone occupies about three external quarters of the sagittal strata corresponding with the external sagittal layer. The caliber of a considerable number of the degenerated fibers is here of medium size, though the coarse fibers are more conspicuous. The internal sagittal layer, which farther up in the occipital lobe hardly exists, and the tapetum remain free from degeneration as soon as the descending and callosal fibers have disappeared. The contours of the degenerated zone of the external sagittal layer are quite sharp against its dorsal and ventral portions left unaltered. They become a little less sharp more occipitalward when the degenerated bundle begins to approach the striate cortex. Along its course occipitalward the visual bundle does not give off any fibers for the parietal or for the occipital cortex until it reaches the level of the striate area.

The further course of the bundle is similar to that in the foregoing experiments. It gradually ascends dorso-medially by describing a spiral turn around the callosal bundle and the lateral ventricle, and finally reaches the upper lip of the calcarine fissure (*Ls* in fig. 75). Here again the degenerated fibers run for a considerable distance in the oral direction inside the thin fiber layer covering the calcar avis and within the white substance of the upper lip before they penetrate in the striate cortex. This is especially the case with fibers destined to supply the bottom of the fissura calcarina which, by running in a retrograde sense, reach the oral beginning of the striate area. Thus a portion of the common single degenerated bundle in this experiment terminates in the upper lip of the calcarine fissure where its fibers enter exclusively the striate cortex. However, in contradistinction to Experiments II and III, the supplied zone in this experiment (*ab* in fig. 75) does not coincide with the whole striate cortex of the upper lip, leaving a narrow strip, the actual "boundary segment" of the striate cortex in that lip (between the arrow and the letter *a*, in fig. 75), with normal fibers. The degenerated bundle of the visual radia-

tion is consequently, not quite identical here with that in Experiments II and III, not being a "boundary bundle," though it becomes so more occipitally (fig. 76). This is in accord with the seat of the lesion in the present experiment which is somewhat below the spot of the lesion in Experiments II and III, that is, closer to the "axial" rib of the fiber fan of the visual radiation (represented by M in fig. 13).

The remaining fibers of the degenerated bundle which do not terminate in the upper lip of the fissura calcarina, proceed occipitalward, and either ascend dorsally, turning partly around the posterior horn of the lateral ventricle and being gradually distributed to the striate cortex covering the dorsal edge of the occipital operculum on both sides (on the internal and on the external face, fig. 76), or they deviate from the common bundle forming laterally to it the stratum extremum of R. A. Pfeifer, from which they are gradually distributed over the external face of the occipital lobe. In the occipital pole the fibers spread out like a fan supplying a segment of the striate area which lines both lips and the bottom of the ascending branch of the calcarine fissure as far as the limits of the striate cortex (compare lower figure in fig. 12). Behind this branch of the fissure on the inner face of the hemisphere the supplied segment of the striate area occupies approximately the dorsal half of the occipital pole. On the lateral face of the hemisphere (upper figure in fig. 12) the supplied segment has the shape roughly resembling a triangle, occupying the larger upper portion of the occipital operculum above the external calcarine sulcus. The anterior boundary of this triangle being parallel to the sulcus simialis (*Ss*) corresponds exactly with the oral boundary of the striate area easily discernible by the presence of the stria Gennari or Vieq d'Azyr (compare fig. 12, with fig. 7, field 17, on the external face of the hemisphere).

It was striking to find in this experiment as well as in foregoing ones that no single afferent visual fiber goes beyond the boundary of the striate cortex (fig. 76). It was also true that no degenerated fibers whatever entered any other segment of the striate cortex (lower lip of the calcarine fissure, lower half of the occipital operculum) except the triangle described above. The shaded area along the main horizontal branch of the fissura calcarina (*Fcalc* in fig. 12) indicates here as in the foregoing experiments merely the longitudinal extent of the supplied zone, the striate cortex being here buried in the fissure. This cortex reaches the free face of the hemisphere only along the ascending and descending branch of the calcarine fissure and, of

course, on the external face of the hemisphere. Both the supplied segments of the striate area, that along the ascending branch of the calcarine fissure and that covering the dorsal edge of the occipital operculum including that on its external face, must be regarded as "boundary segments" (on the lateral face as far as the anterior boundary along the *fissura simialis* is concerned). The region of the striate area which receives degenerated fibers in this experiment is larger than the supplied region in both Experiments II and III. It is, however, considerably smaller than the supplied region in Experiment I, the latter representing the entire visual cortex except that in the lower lip of the calcarine fissure (compare fig. 12 with figs. 1, 2, 3, and 7); and is also less than the region determined in Experiment V-A (fig. 4).

No visual afferent fibers were seen in the present experiment to turn into the corpus callosum in order to reach the opposite hemisphere.

When comparing this experiment with those described previously it is apparent that the bundle degenerated here becomes a "boundary bundle" more caudad around the posterior end of the calcarine fissure, and over the occipital lobe. More oral this bundle is, as a matter of fact, the next inward to the actual "boundary bundle" (with respect to the axis of the visual radiation) which supplies the upper lip of the undivided portion of the calcarine fissure (the latter degenerated in both Experiments II and III). This signifies a longitudinal, but at the same time toward the occipital pole a somewhat oblique ascending (in the upper lip) or descending (in the lower lip of the calcarine fissure) arrangement of the individual narrow triangular segments of the striate cortex corresponding with the individual fiber bundles of the visual radiation. Except for the most dorsal and the most ventral "boundary bundle" of the visual fiber fan and their cortical segments all other segments reach, accordingly, the posterior boundary of the striate area with their caudal extremities only; whereas their pointed oral extremities are pushed somewhat inward by the more dorsal (in the upper lip), or the more ventral segments (in the lower lip of the calcarine fissure).

EXPERIMENT V-A

In this experiment the attempt was made to interrupt the macular fibers of the visual radiation separately and to study their course, position, and cortical termination with the help of Marchi's method.

Fourteen days later the animal was killed. By a single, sharply delimited lesion in the left hemisphere of a young Java monkey (small coarsely dotted area in fig. 4 and *L* in fig. 13), beginning with a superficial damage to the most posterior portion of the middle temporal convolution, the intermediate or the perpendicular branch of the visual radiation (*vr* in fig. 13) was interrupted. (For reference to the anterior part of the lesion in the same case, causing a portion of the thalamo-cortical radiation to degenerate see Somato-sensory System, Chapter V, Experiment V-A). The degenerated fibers, forming at first a fairly sharply delimited segment within the vertical or perpendicular branch of the visual radiation (*M* in 2 and 3 of fig. 13), were easily pursued—on sections of the continuous series, well stained according to Marchi's method—along their course occipitalward to their termination in the cortex of the occipital lobe (4, 5 and 6 of fig. 13). They all enter the striate area, or field 17 of Brodmann, exclusively, and only that portion of the field covering the lateral face of the occipital lobe situated behind the ascending and descending branches of the calcarine fissure (area of the occipital lobe in fig. 4 shaded with continuous and broken horizontal lines). A narrow zone of the opercular striate cortex in the dorsal and the most anterior part of the occipital operculum receives few or none of the degenerated fibers in the present experiment (the narrow finely stippled triangular zone of the occipital operculum in the upper figure of fig. 4). This zone of the macular cortex with its afferent visual fibers remaining normal, continues with the striate area lining the upper lip of the calcarine fissure on the inner face of the hemisphere (*Fcalc* in fig. 4). The striate area lining the floor and the lower lip of the calcarine fissure is also completely devoid of any of the degenerated afferent visual fibers. Of the entire striate cortex within the calcarine fissure, the only portion where there are degenerated fibers is that portion lining the ascending and descending branches of this fissure, especially around the ascending branch; but even here only the striate cortex behind the mentioned branches is filled with black dots and particles, the rest of the striate cortex in front of both ascending and descending

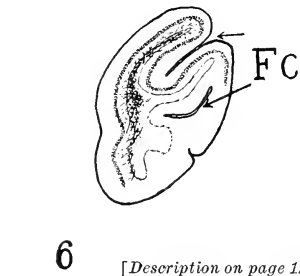
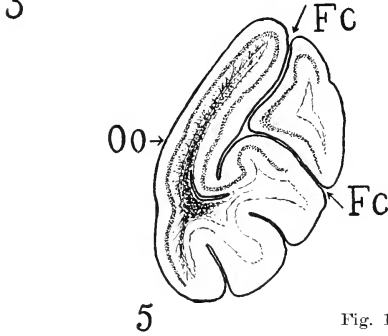
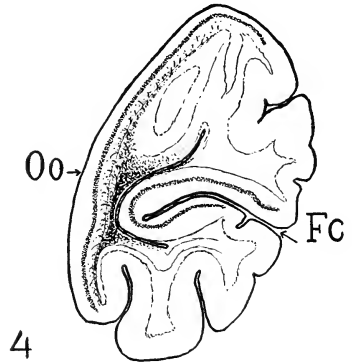
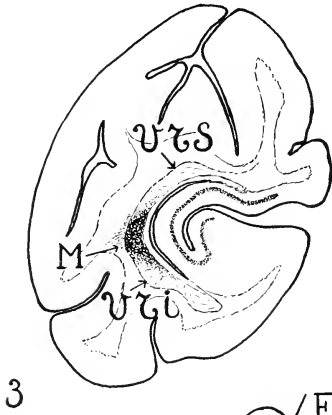
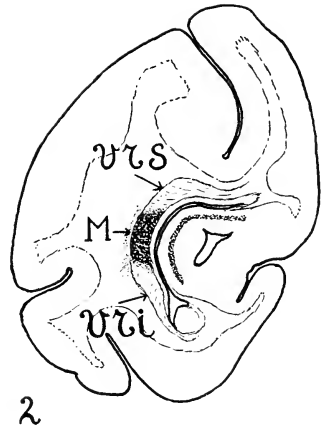
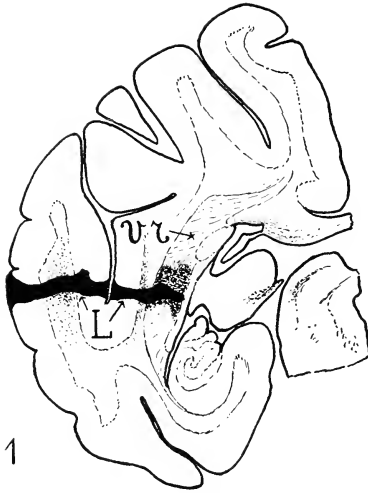


Fig. 13

[Description on page 127]

branches remaining free (lower figure in fig. 4). Degenerated fibers entering into the macular cortex are everywhere abundant, especially around the sulcus carcarinus externus of Cunningham-Elliot Smith. These fibers are mostly delicate.

Both the superior and inferior horizontal branches of the visual radiation contain none or only a few scattered degenerated fibers, especially none corresponding with the main undivided portion of the calcarine fissure. Consequently in this experiment, the scattered or solitary degenerated fibers, without mentioning the absence of the compact bundles of these found in the preceding four experiments, reach neither the upper nor the lower lip of the calcarine fissure.

The peri-parastriate area of Elliot Smith, the field 18-19 of Brodman, remains completely free from any degenerated fibers, these strictly respecting the boundaries of the striate cortex, as in the preceding experiments.

A few of the degenerated fiber bundles enter the opposite hemisphere through the corpus callosum. They consist of thin fibers interrupted in the tapetum by the same lesion that interrupts the macular fibers of the external sagittal layer. These fibers evidently belong to the callosal system.

As the present experiment well demonstrates, the intermediate or the perpendicular branch of the visual radiation neither mingles with the upper nor with the lower horizontal branch of the radiation. Its course is directly toward the occipital pole in contradistinction to both horizontal branches which reach their respective lips of the calcarine fissure by devious ways: the upper one bends gradually in a spiral-like fashion around and above the upper edge of the lateral ventricle, and the lower one goes below the lower edge of the same ventricle. (Compare Chapter XVI.) The macular branch of the visual radiation faces during almost its entire oral-caudal course the posterior horn of the lateral ventricle on its lateral side. This branch enters solely the portion of the striate area covering the occipital operculum and the

Fig. 13, Experiment V-A. This figure demonstrates the position of the macular portion of the visual radiation, the so-called "macular bundle" (*M*), within the sagittal fiber layers (*vr*) of the occipital lobe, degenerated after a localized injury to these layers (*L*), and the course and entry of the macular fibers into the macular portion of the striate area covering the lateral face of the occipital operculum (*Oo*) and the tip of the occipital lobe. The macular portion of the visual radiation (*M*) forms its intermediate or perpendicular branch; the superior (*vrs*) and the inferior horizontal branch (*vri*) of the visual radiation which, in the monkey, enter into the upper and lower lip of the calcarine fissure (*Fc*) respectively, retain in this experiment normal fibers. (Compare with fig. 4; for explanation see Chapter XVI and XVII.)

pole of the occipital lobe behind the calcarine fissure. This same portion of the striate area when destroyed is followed by degeneration of the intermediate segment of the external geniculate body, where, according to Brouwer and Zeeman, macular fibers of the retinae terminate. (In Experiment V-c the six small lesions of the occipital opercula caused degeneration in the intermediate segments of the external geniculate bodies, figs. 17, 18; in Experiment V-b where only the upper and lower lip of the calcarine fissure was damaged this particular segment remained almost intact, figs. 14, 15, 16; see also Heuven.) The conclusion from the present experiment is, that the macular portion or segment of the visual radiation—the so-called “macular bundle”—runs in an isolated way from its origin in the external geniculate body to its termination in the macular portion of the striate area. It is probable, however, that the actual macular portion of the visual radiation in the monkey is slightly larger than determined here, especially dorsally, since in the most dorsal portion of the macular cortex most of its fibers remained normal. It is also clear that the macular fibers strictly avoid both horizontal branches of the visual radiation and do not enter either of the lips of the calcarine fissure or its bottom, with the exception of the most posterior portion around both the ascending and descending branches. The present experiment by proving in a clear and simple way the true position and the actual course of the “macular bundle” demonstrates not less clearly the fallacy of the concept held by some contemporary investigators: that the macular fibers form either the most dorsal or the most ventral bundle of the visual radiation and that they reach in some unknown and complicated way, perhaps by passing through the fiber layer covering the calcar avis, the macular cortex.

Of the descending fibers, interrupted in the sagittal strata of the parietal lobe, only those entering the pulvinar of the thalamus and reaching the superior colliculus of the midbrain degenerated. No degenerated fibers were seen to enter the external geniculate body itself, though the sagittal strata were damaged not far from that body. The belief that there exists an extensive fiber system descending from the striate cortex and terminating in the external geniculate body seems to need further experimental confirmation.

It is well known from comparative studies that in the course of evolution that portion of the striate area of the lower primates covering the lateral face of the occipital lobe—the so-called operculum occipitale (Brodmann)—was gradually pushed back and inward and

folded in, due to the more rapid expansion of the non-receptive areas of the parieto-occipital lobes (Elliot Smith, Brodmann 1909, Ariens Kappers 1921, Kuhlenbeck; for somewhat different explanation see Economo 1930). In higher primates, in anthropoids, and in man, that portion lines approximately the posterior one-third or two-fifths of the calcarine fissure and covers the tip of the occipital lobe. If one can accept essentially the same arrangement of the visual radiation in anthropoids and in man, as found here to be valid for the lower primates—and no plausible argument against this can be produced—one must conclude that also in higher primates the macular portion of the visual radiation has a course directly to the occipital pole and to the posterior portion of the calcarine fissure, running along the lateral face of the posterior horn of the lateral ventricle, touching dorsally those fibers which gradually enter the upper lip of the calcarine fissure, and ventrally those destined for the lower lip. There is, however, in anthropoids and in man this difference in comparison with lower monkeys: in the former the macular fibers eventually turn medially around the posterior end of the lateral ventricle to reach the posterior portion of the calcarine fissure; while in the lower primates, where the greater portion of the macular cortex is on the lateral face of the occipital lobe, the majority of the macular fibers turn laterally. (On the visual radiation in general and on the macular pathway in particular compare Chapter XVI.)

EXPERIMENT V-B

In this experiment the intent was to perform an isolated injury to the lower lip of the calcarine fissure, and in such a way to produce the retrograde changes in the lateral geniculate body according to Nissl's method of the "primary irritation of cells" or of the "retrograde degeneration." In a young Java monkey the left occipital lobe was luxated and the lower lip of the fissure damaged by means of a lancet (lower figure in fig. 14).

Twenty-two days later the animal was killed. A careful macroscopic and microscopic examination of an interrupted series through the left occipital and parietal lobes, well stained with thionine blue according to Nissl, revealed two injuries: a small superficial one close to the ascending branch of the calcarine fissure strictly limited to the cortex lining the inner face of the hemisphere and hardly reaching the subcortical white matter (marked with a double cross,

fig. 15), and another large injury to the lower lip of the calcarine fissure slightly damaging the cortex and also penetrating deep into the subcortical white matter and cutting through the lower horizontal branch of the visual radiation (marked with an asterisk, fig. 15). The small injury damaged, accordingly, a small segment of the striate cortex immediately in front of the ascending branch of the calcarine

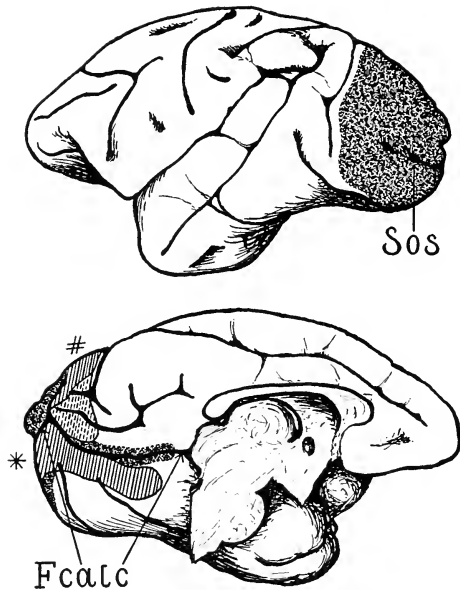


Fig. 14, Experiment V-B. External (upper figure) and internal (lower figure) face of the monkey's hemisphere (left) showing the location and extent of the injuries (areas shaded with line) to the striate area and to the visual radiation, in this experiment. Small superficial lesion marked with a double cross; large lesion marked with an asterisk. Stippled area represents the striate area remaining normal. Calcarine fissure (*Fcalc*); external calcarine sulcus (*Sos*). (Compare with fig. 15, 16.)

fissure; the large ventral lesion, extending along almost the entire main undivided portion of the calcarine fissure, interrupted a solid portion of the ventral branch of the visual radiation and thus separated it from its terminal cortex in the lower lip of the calcarine fissure.

The left external geniculate body studied with particular care on a continuous series, well stained with thionine blue according to Nissl, showed two separate zones where the nerve cells degenerated (fig. 16).

The small zone in the inner or medial segment of the body (marked with a double cross) confined to the superficial cell layers was found on a few sections only in the posterior portion of the body, and the large degenerated zone in the outer or lateral segment of the body

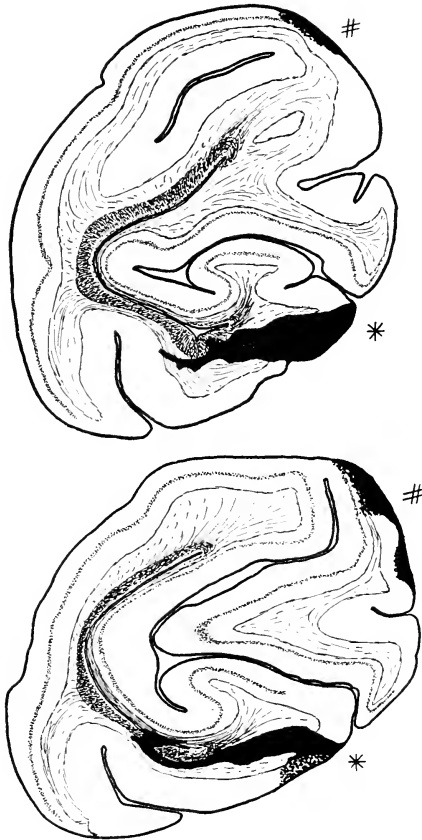


Fig. 15, Experiment V-B. Sections through the occipital lobe of figure 14. The destroyed portions represented in solid black; the upper and smaller lesion marked with a double cross; the lower and larger lesion marked with an asterisk. The visual radiation visible as a thick semilunar fiber layer in the center of the figures encircling the calcarine fissure. The lower lip of the fissure is undermined, the ventral horizontal branch of the visual radiation is interrupted and its fibers, streaming into the lower lip of the fissure, are cut off. The striate cortex is indicated by a dotted stripe.

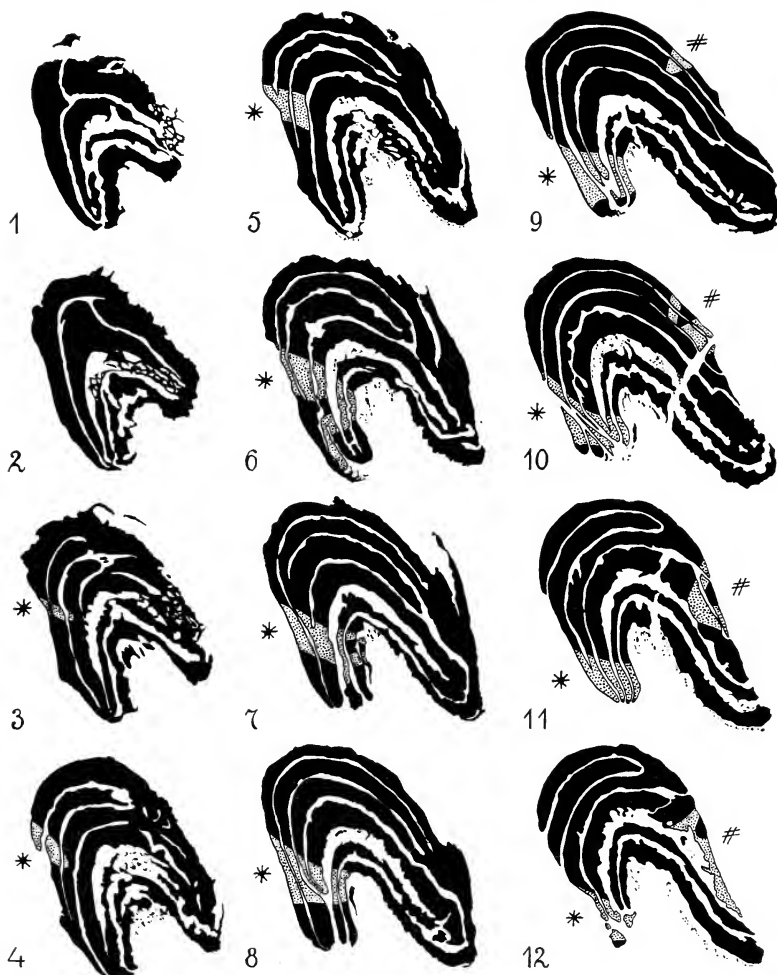


Fig. 16, Experiment V-b. This figure shows the sections through the left external geniculate body beginning with the most anterior (oral) section (1), and the most posterior (caudal) section (12). Left sides of the figures are lateral, right sides are medial, close to the thalamus. Stippled portions represent segments where nerve cells degenerated; black portions those with normal cells. In agreement with two lesions of the striate area or of the visual radiation (14, 15) (compare figs. 14, 15) two degenerated zones were found: A small one in the inner segment of the external geniculate body (marked with a double cross) and a large zone in the outer segment of the body (marked with an asterisk).

(marked with an asterisk) was found to pass through all cell layers of this particular segment down to the most ventral layers containing large nerve cells. Both degenerated zones have no stable position within the nucleus inasmuch as they both gradually descend from caudal sections where they appear (3 and 9 in fig. 16) to the ventral edge of the nucleus in the oral direction (12 in fig. 16). Thus, the large degenerated zone is closer to the apex of the nucleus (to its dorsal tip) on oral sections, being confined on caudal sections to the ventral tip of its lateral segment. Also on oral sections this zone does not penetrate through all cell layers (3, 4, 5, in fig. 16) reaching the ventral layers containing large cells on subsequent and more caudal sections (6-12 in fig. 16). It is remarkable that in both zones the boundary lines between the normal and degenerated portions of the cell layers are quite sharp and that the boundaries pass through several cell layers in the same direction, as the accompanying fig. 16 well demonstrates. (Compare E. Vries and Heuven). The nerve cells in both degenerated zones appear reduced in number, are pale and shrunken, and show signs of phagocytosis, while the nuclei of glia cells are increased in number. Also no normal nerve cells were found in the degenerated zones, the degeneration here being complete.

The present experiment showed that: (a) After a small lesion of the striate area on the inner face of the hemisphere just in front of the ascending branch of the calcarine fissure (in fig. 14 marked with a double cross and shaded with continuous perpendicular lines; also fig. 15), a small portion of the ipsilateral external geniculate body, which occupies a part of the inner segment of that body where according to Brouwer and Zeeman optic fibers from the upper extramacular homonymous quadrants of both retinae terminate, degenerated; and that (b) after the damage to the lower horizontal branch of the visual radiation (shaded area in fig. 14 marked with an asterisk which, however, shows only the hidden striate area projected upon the surface) a comparatively large portion, almost the entire lateral segment of the external geniculate body where, according to Brouwer and Zeeman, optic fibers from the lower extramacular homonymous quadrants of both retinae terminate, degenerated. It is, however, probable that in our case a small number of macular fibers—those entering the striate area close to the posterior end of the calcarine fissure—were also interrupted, and the degenerated zones in the external geniculate body to a small extent spread over into the macular segment of that body.

EXPERIMENT V-C

In this experiment the intent was to make several small injuries to the macular portion of the striate area in both hemispheres and to study the number, size, extent, and above all the position of the degenerated zones in both external geniculate bodies. It was hoped that if the cortical injuries were sufficiently small and confined to the striate cortex, and sufficiently isolated from one another, this would be reflected in the size, location, and arrangement of the degenerated zones in the geniculate bodies. Since the arrangement of the cortical injuries could easily be determined this would give, it was expected, enough data to find out whether the "figure" or the "configuration" of the macular cortical lesion was preserved in the macular segments of the lateral geniculate bodies.

For this purpose the following experiments were performed on a half-grown *Macacus rhesus*:

(a) In the left hemisphere three small lesions of about equal size and almost equally distant from each other were made in the macular portion of the striate area, two along the simian sulcus (*b* and *c* in 1 and 2, fig. 17), and the third along the lower limit of the macular cortex (*d* in 1 and 2, fig. 17); in this same hemisphere a fourth and considerably larger lesion was made in the upper edge of the occipital operculum extending as far back as the occipital pole (*a* in 1, 2, and 6, fig. 17).

(b) In the right hemisphere one small lesion was made in the upper portion of the occipital operculum (marked with a double cross in 3 and 4, fig. 17); a second and a more extensive lesion was made in the lower third of the occipital operculum (marked with an asterisk in 3 and 4, fig. 17).

Observation of the visual behavior of the monkey beginning with the fifteenth day after the operation revealed a general disturbance of the vision. Besides that, hemianoptic symptoms to the right were apparent: the monkey never noticed a morsel of food offered from the right side; but he saw it immediately when it reached the middle sagittal plane, or when it was offered from his left side (he reached for it with his left hand). However, he usually passed the object to the left and also miscalculated the distance. He grasped the object with the hand in a clumsy way, and he climbed slowly, cautiously, hesitatingly, in a quasi-atactic manner. This was understood

to be due to the impaired vision, since otherwise the monkey did not show disturbances of the sensory-motor apparatus. With respect to his general behavior the monkey appeared passive; it was difficult to arouse his interest as soon as his hunger was satisfied and he had

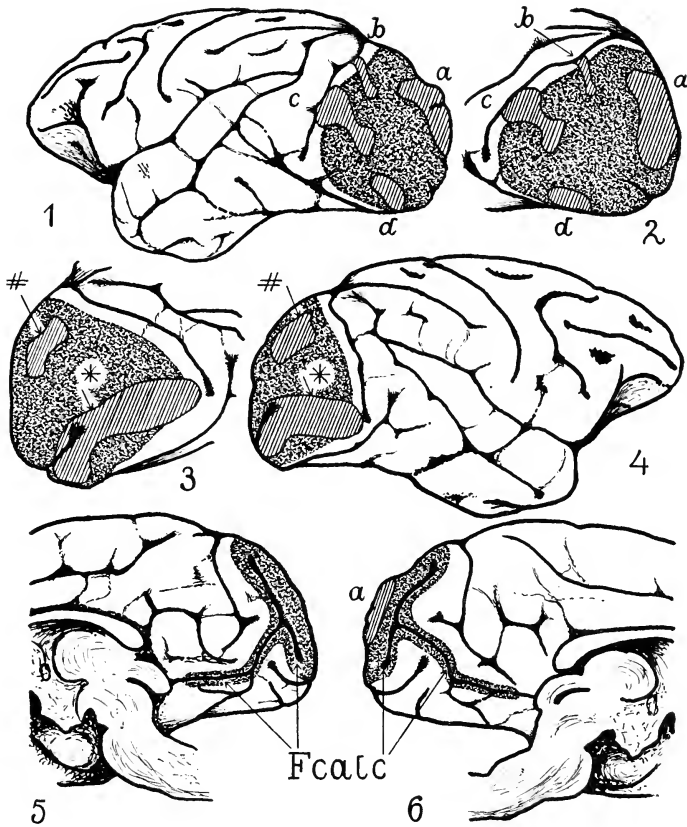


Fig. 17, Experiment V-c. This figure shows outer face (1, 2) and the inner face of the left hemisphere (6); outer face (3, 4) and the inner face of the right hemisphere (5). Areas shaded with lines represent lesions; stippled areas are portions of the striate areas remaining normal. In the left occipital operculum there are four separate lesions: three small ones (b, c, d), and a larger one (a); in the right occipital operculum one small lesion (marked with a double cross) and a large one (marked with an asterisk). (Compare with fig. 18.)

retired to his corner of the cage. (The monkey was in a poor condition during the first five days because of erysipelas of the face.) Three days later the signs of hemianopsia on the right side were again apparent. The monkey appeared to be unable to understand the meaning of threats, not reacting to these with either the movements of the eyes or of the head, or with attempts to escape, as do normal animals. Had it not been known that his visual cortex on both sides was damaged one would have regarded his disturbance as the visual agnosia. On the next day the same symptoms were again apparent; mainly hemianopsia to the right and quasi-agnostic visual disturbances. When a piece of banana was offered to him he reached for it as soon as he noticed it (after a while) but usually missed it, touching or grasping the fingers of the hand offering food; and only gradually by "touch" did he find the food. From this observation one gets the impression that the monkey had a distinctive defect of the visual localization due to the lesion of that portion of the visual cortex which represents points of fixation, besides other perceptive disturbances due to multiple scotomata. There was also a change in the character of this animal: he had lost the fear which characterizes most monkeys, who, as a rule, immediately become vigilant and try to escape into the most distant corner of the cage as soon as one enters the room or approaches the cage, or even makes an unexpected move. Three days after that homonymous hemianopsia on the right side was again present, though this seemed to be incomplete. At any rate, the monkey ignored the objects appearing on his right side, while as soon as they appeared on his left side he reached for them. When reaching for the food he exclusively used his left hand, that is the hand ipsilateral with the halves of his visual fields still functioning fairly well. In contrast to that he used his right hand quite well in such acts where the visual control was not required to a great degree, or when it was required in a more summary way, as for example in slow climbing, in scratching the fur, and the like. When grasping for the food the monkey made the same error as before: he reached too far as a rule, at the same time he usually missed the object to his left. He likewise exhibited the same disturbance in fixing (seeing, recognizing, identifying?) the pieces of food: when one held a piece of banana toward him he at first touched the hand or tried to grasp the fingers, and then, only by slowly feeling and searching the hand did he find the banana. This was thought to be due to the fact that because of the numerous gaps in his visual fields, the differences in color and

shape, etc. between the piece of banana and the details of the hand were too slight for the food to be correctly seen, or recognized, or localized. The whiteness of the hand and of the piece of food merged into one single "figure," and because the hand represented a larger part of the "figure" there was a greater chance that he would touch the hand rather than the food. Nevertheless, sometimes after from five to ten attempts he aimed better and reached directly for the food. This rather indicated a simple disturbance of the visual perception, of localization and fixation, since the understanding of the "meaning" of food ("something to eat") was evidently only retarded but not essentially impaired. The process of recognizing and identifying appeared to be distinctly slowed down. The protective eye reflexes were not always present, especially after prolonged exercise, but they could almost always be evoked after a pause. They were present on both sides. A difference in the size of the pupils was not noticed. The change in "character" of this monkey was always the same: while the normal Macacus rhesus follows all changes in his surrounding with complete distrust and almost invariably reacts with fear and flight, our monkey became "docile," did not run away, and regularly took the food from the hand. It is entirely conjectural whether this change was due to the defect in simple perceptive visual processes because of the incompleteness of his visual impressions, or was due rather to the disturbance of higher cognitive and similar functions. (The latter assumption would seem more probable since the monkey could very well recognize various sounds, especially "signals of danger" emitted by his ever watching companions).

As is clear from the foregoing description there were in the present experiment manifest signs of a right homonymous hemianopsia which was probably due to the more extensive damage to the left macular cortex, besides other symptoms due to the fact that the right macular cortex was also damaged.

Twenty-three days after the operation the animal was killed. The study of the left occipital lobe, stained according to Nissl's method, revealed three small injuries and a large one of the occipital operculum (fig. 17). The injury (*b*) is almost purely cortical and is sharply delimited; the injury (*c*) is also well circumscribed though it penetrates slightly into the subjacent white matter and interrupts there a small bundle of the afferent visual fibers; because of the arrangement of these fibers in the sagittal direction at the point of their interruption, it was assumed that though the segment of the

striate cortex de-afferented in such a way was slightly larger, it was in part identical with the lesion (*c*). The third small injury (*d*) also slightly reaches into the white subcortical substance, but is otherwise well delimited; this lesion can also be considered as an equivalent of a purely cortical lesion since it is located at a considerable distance from the sagittal strata of the occipital lobe and, consequently, interrupts merely a bundle of fibers streaming into the cortical segment indicated by (*d*) and, at most, into its nearest vicinity. The fourth and largest injury (*a*) not only destroys directly a considerable portion of the macular cortex in the upper and central half of the macular region including the tip of the occipital lobe behind the calcarine fissure, but penetrates as well into the white substance where it interrupts fibers destined for the striate cortex lining the ascending branch of the calcarine fissure (its posterior lip).

The left external geniculate body studied on sections of a continuous series stained according to Nissl's method (left eight figures in fig. 18), in agreement with the number of the lesions, showed also four distinctive zones where the cells degenerated: one large, and three small ones. The large zone (*a*) appears on most oral sections as a narrow triangle in the upper portion of the nucleus pointing with its sharp angle toward the hilus of the nucleus without, however, reaching it (*1* in the left upper corner). This zone on subsequent caudal sections becomes gradually larger in width and extends farther down to the hilus and finally reaches the ventral layers containing large cells (*2-7* in the first and second row from the left). On the whole, this degenerated zone remains strictly confined to the intermediate or macular segment of the lateral geniculate body. The three small degenerated zones, corresponding with the three small lesions of the most anterior portion of the opercular striate area (which we can consider the "posterior" limit of the striate area, if we imagine the occipital pole pushed back and attaining the position on the tip of the occipital lobe, as found in human brain) appear only in the posterior half of the lateral geniculate body (*b, c, d* in *6-8* in the second row from the left). At first appear two small wedge-shaped zones in the tip of the nucleus (*b, c*, in *6*, second row from the left). Both zones are triangular in shape, pointing with their sharp angles toward the hilus of the nucleus without reaching it, or merging with the vestige of the large zone (*a*) confined here to the lower portion of the intermediate segment of the nucleus and just reaching the hilus. On the sections farther caudal the third small degenerated zone appears (*d* in

7, second row from the left). All three last mentioned small degenerated zones are well delimited and mutually separated by zones containing normal cells. Only in the most caudal sections the zones (*b*) and (*c*) merge into one zone ($b + c$ in 8, second row from the left) which is probably due to the fibers being interrupted beneath the lesion (*c*). A more detailed analysis of the position, size, and so forth, of the three small zones reveals that the zone (*b*), the smallest in this experiment, in accord with the smallest lesion (*b*, fig. 17) occupies a position closest to the internal brim of the lateral geniculate body (right contours in fig. 18). This zone is closest to the internal segment of the body from which fibers arise for the upper lip of the calcarine fissure—a fact that is in good accord with the position of the lesion, the latter also being closest to the upper lip. The next small zone (*c* in fig. 18) has already a more lateral position, while still more lateral is the third small zone (*d*) which is close to the lateral segment of the lateral geniculate body. The position of the latter zone agrees with the position of the lesion (*d* in fig. 17) which is also closest to the lower lip of the calcarine fissure. Thus the position and the arrangement of all of the three small degenerated zones within the intermediate segment of the lateral geniculate body indicates a regular, orderly projection of small sectors of that particular segment of the body upon equally regularly arranged small sectors of the macular cortex. The large zone (*a*), due to the fact that its lesion is also in a more “anterior” position (imagining the striate area of a monkey stretched into the sagittal plane to conform to conditions in the human brain), is also in the anterior portion of the lateral geniculate body. This zone although placed in the intermediate segment of the body probably does not correspond entirely to the macula lutea proper which we must imagine to occupy the most “posterior” position in the striate area (in monkey close to the simian sulcus, in man around the pole of the occipital lobe), but to its immediate neighborhood. Also, this zone enters into the ventral cell layers around the hilus of the lateral geniculate body, which according to all probability, is the consequence of fibers being interrupted by the lesion (*a*) bringing impulses from the more “peripheral,” that is perimacular regions of the retinae and, in the monkey, entering the posterior portion of the calcarine fissure. Common to all of the four degenerated zones is their location in the intermediate or macular segment of the lateral geniculate body. The zones leave intact both the external and internal “peripheral” segments of that body, which fact is in a good accord

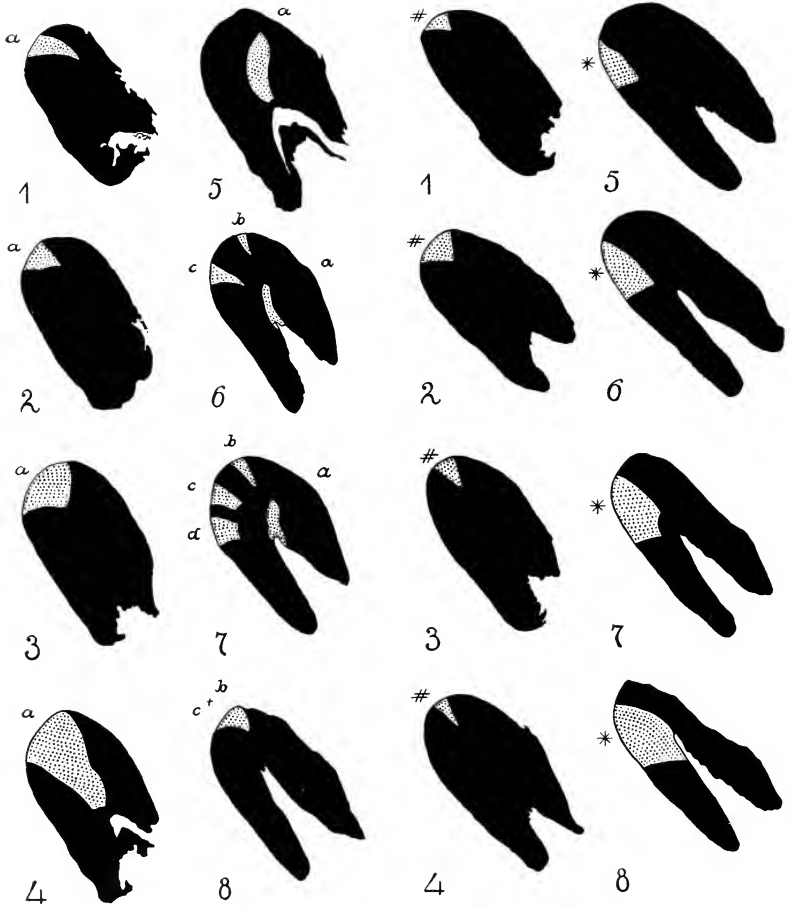


Fig. 18, Experiment V-c. This figure shows sections through the left external geniculate body (left two vertical rows) and through the right external geniculate body (right two vertical rows). Anterior (oral) sections (1, 1), posterior (caudal) sections (8, 8). Left sides of the figures are lateral, right sides are medial, close to the thalamus. Stippled portions represent segments where nerve cells degenerated; black portions, those with normal cells. In agreement with four lesions of the striate area of the left occipital operculum (fig. 17) four separate degenerated zones were found in the left external geniculate body (left 1-8, zones a, b, c, d); in the right external geniculate body, in agreement with the two lesions of the striate area of the right occipital operculum (fig. 17), two separate degenerated zones were found (right 1-8, zone marked with a double cross, and with an asterisk).

with the finding that all four lesions of the left hemisphere are confined to the occipital operculum, and none of the fibers destined for the upper and for the lower lip of the calcarine fissure proper were interrupted. (Compare Experiment V-B.)

The right occipital lobe studied in sections stained according to the method of Nissl revealed two separate and well-delimited lesions in the occipital operculum. The ventral—and larger—lesion occupies approximately the lower half of the operculum in its entire longitudinal extent (shaded area marked with an asterisk in 3 and 4, figure 17). Beginning with its anterior end close to the extremity of the simian sulcus it extends as a broad slightly curved stripe along the lower limit of the opercular striate cortex and along the collateral sulcus toward the external calcarine sulcus as far back as the tip of the occipital lobe. This extensive lesion at about the middle of its longitudinal extent penetrates deep into the subcortical white substance and even reaches the sagittal strata where it interrupts approximately the lower half of the perpendicular or vertical macular branch of the visual radiation (identified as such in Experiment I-IV, and especially in Experiment V-A; compare *M* in figure 13). One has, therefore, to assume that the effect of both the cortical and subcortical lesion is here approximately the same: the destruction of the lower half of the macular radiation and of the lower half of the macular cortex. The upper and the smaller lesion occupies a portion of the upper half of the opercular macular cortex close to its dorsal limit (marked with a double cross in 3 and 4, fig. 17). This lesion remains mostly cortical and penetrates only slightly into the subcortical white substance. Its effect must be purely local, since the afferent visual fibers damaged by it are here already far distant from the sagittal strata. The rest of the striate area, above all the entire calcarine fissure, as well as both the upper and the lower horizontal branches of the visual radiation which terminate there, remain perfectly normal in their entire extent. Even in sections where the lower larger lesion reaches the sagittal strata, the fiber layer covering the calcar avis (that is, the main horizontal portion of the calcarine fissure which represents "peripheral" retina), because it is situated inward from the posterior horn of the lateral ventricle, remains absolutely intact. (For explanation see Chapter XVI.)

The right external geniculate body studied in sections of a continuous series stained according to Van Gieson's method (right eight figures in fig. 18), disclosed two distinctive zones where the cells

degenerated: a large zone and a small one. Thus the number of zones in this experiment also agrees with the number of lesions. The large zone occupies about the lateral half of the intermediate or macular segment and is found on sections through the posterior third of the lateral geniculate body (marked with an asterisk in 5-8, last row to right). This zone has in more anterior sections a triangular shape with the sharp angle pointing toward the hilus of the nucleus which is, however, reached in most posterior sections only. The small degenerated zone occupies exactly the tip of the lateral geniculate body, and is of triangular shape with the sharp point turned toward the hilus of the nucleus although it does not reach it. This zone is found in the anterior or oral half of the lateral geniculate body (marked with a double cross in 1-4 in the second row from the right, fig. 18). Here, too, both degenerated zones occupy the intermediate or macular segment of the lateral geniculate body, which again agrees with the position of both lesions in the macular cortex over the occipital operculum and in the macular portion of the visual radiation. In particular, the position of the small degenerated zone (double cross) is identical with a portion of the degenerated zone (*a*) in the left hemisphere, in agreement with the smaller size of its lesion; while the larger degenerated zone (asterisk) partly corresponds with both small degenerated zones (*d* and *c*) in the left hemisphere which agrees with the position of its lesion.

The general result of both these experiments in the left and right hemisphere is that all of the six degenerated zones are placed in the intermediate segment of the lateral geniculate body where, according to Brouwer and Zeeman's experiments, macular fibers from both retinae terminate. This is in agreement with the fact that all six lesions were located in the macular portion of the striate area or close to it. (Compare Experiment V-B, which is the reverse of the present experiment.) It is also evident that there exists a fair degree of correspondence between the number, size, and position of the small degenerated zones in the lateral geniculate body and in the striate cortex of the corresponding hemisphere. The conclusion seems to be that each small segment of the lateral geniculate body has its own representation in the visual projection cortex of the same side, and does not mingle with its neighbors. In other words, there exists a faithful projection of the lateral geniculate body and thus of the hemiretinae upon the striate area, which renders possible a faithful preservation of "figures" in the visual acts. It is also clear that if the macular

segment of the lateral geniculate body would send a part of its fibers to the opposite striate area this would in our experiments have most probably resulted in a "blurring" or in a complete obliteration of the "figures" of the degenerated zones in both lateral geniculate bodies.

EXPERIMENT V-D

The purpose of this and of the following experiment (V-E) was to destroy as completely as possible the striate area of the one occipital lobe, and in this way, produce the "primary irritation" or "retrograde degeneration" of all cells whose fibers terminate in the removed portions of the cortex (Nissl). Here the chief interest was concentrated upon the questions: (a) Do all nerve cells of the ipsilateral external geniculate body degenerate, or only some of them? (b) Do any of the nerve cells of the opposite external geniculate body degenerate? It was obvious that if all cells of the external geniculate body send their axis cylinders to the striate area of the same side, and consequently none of the fibers of the visual radiation terminate in the pulvinar, in the tectum, or in the striate area of the opposite side ("fasciculus arcuatus corporis geniculati lateralis" of Ferraro, "fasciculus corporis callosi cruciatus" of Niessl von Mayendorf and of R. A. Pfeifer), and if there are no intercalated cells in the external geniculate body, as it was supposed ("Schaltzellen" of Monakow), a complete degeneration of nerve cells of that nucleus ipsilateral with the destroyed striate area was to be expected. It was equally clear that if some of the fibers of the visual radiation terminate in the opposite occipital lobe, this would be manifest by a partial degeneration of the cells of the external geniculate body opposite to the destroyed striate area.

In a young Java monkey the left occipital lobe was completely removed by means of a thermocautery. Twenty-four days later the animal was killed. No open wound of the skin, no pus or inflammation under the skin or beneath the bone flap was found. The left occipital lobe was found to be entirely absent (fig. 19); the dura was slightly adhering to the surface of the defect and under the dura covering the defect a small quantity of a milky fluid was found (probably the cerebrospinal fluid mixed with the detritus of the disintegrated nervous substance). Macroscopically and microscopically the entire striate area of the left occipital operculum and that of the posterior half of the calcarine fissure was absent, but the anterior half of the fissure—

with the striate area lining it—remained intact. (Compare different result in the following Experiment V-E.) Thus the entire macular cortex and approximately the half of the “peripheral” striate cortex of the left hemisphere were removed in this experiment. In addition to that the upper half of the area peri-parastriata on the lateral face

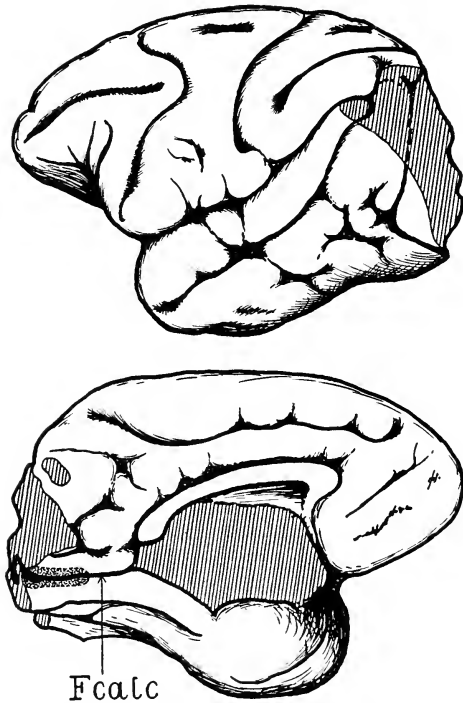


Fig. 19, Experiment V-D. External (upper figure) and internal (lower figure) face of the monkey's hemisphere where the occipital lobe was completely removed. Areas shaded with lines represent cut surface of the occipital lobe, and after the removal of the between brain. The preserved anterior half of the striate area is represented by a narrow stippled stripe along the calcarine fissure (*Fcalc*). In this experiment the external geniculate body degenerated to a greater extent on the same side, the opposite body remained normal.

of the left hemisphere, except its portion within the simian sulcus, was superficially damaged. Over the inner face of the hemisphere the dorsal half of the area peri-parastriata was almost entirely destroyed, while its ventral half probably escaped. The field 7 over

the inferior parietal (supramarginal) convolution was slightly damaged. The rest of the left hemisphere and the entire opposite hemisphere did not show any changes whatever.

Immediately after the operation the pupil ipsilateral with the damaged hemisphere was found to be dilated (or the opposite pupil constricted). Although the animal was a husky one, the operation proved to be a severe shock. It was doubtful whether the monkey ate and drank during the first few days after the operation. Ten days later the monkey was still dull and shy. There was no difference in the size of the pupils so far as it was possible to ascertain. Three days later the monkey successfully gathered "lice" and dandruff from his companion with both hands, snatching them with his lips. In collecting food, climbing, and like activities, he used both hands. On the following day the monkey promptly turned his head to the right from which the visual stimuli came. He was constantly occupied in catching the "lice" of his companion, and he did this with interest. One day later he saw to the right as well as to the left, though it was questionable whether he directed both eyes correctly toward the objects. A day later he certainly preferred the pieces of the carrot falling into the left halves of his visual fields. The pieces of food falling into the right halves of his visual fields up to the median sagittal plane he did not consider. The monkey did not even look to the right side, which to him probably appeared "empty." In picking up the morsels he mostly used his left hand; on other occasions, however, he used both hands. Two days later Dr. H. Klüver found a homonymous hemianopsia on the right side with a fair degree of certainty. This was established by larger pieces of apple (2-3 cm.) and by smaller pieces (1 cm.) and also by peanuts, placed two at a time on a black cardboard. The monkey invariably chose the pieces falling into the left halves of his visual fields. Three days later the monkey again, as several times before, appeared to see to the right also. This was determined, however, by a simple observation of the animal picking the food and moving around in the cage. Two days later the homonymous hemianopsia on the right side was again apparent. The waving of the hand to his right remained unnoticed. When taking a peanut from its shell he held it with both hands, tore the pieces of the shell with his teeth, held the nut correctly with his fingers, and carried it with his right hand to the mouth. In general the monkey appeared passive, almost stupid, was constantly terrorized by other companions, though he in no way appeared physically weak.

From the above description it seems fairly certain that the visual disturbance in this experiment was that of a hemianopsia on the right side although the same was probably incomplete, due to the incomplete destruction of the left-sided striate area.

Both external geniculate bodies including the entire betweenbrain and the adjacent portion of the midbrain were cut in a continuous series and stained with thionine blue according to Nissl's method.

A careful examination of the entire well-stained series revealed: (a) a complete degeneration of all the nerve cells of the external geniculate body ipsilateral with the damaged left hemisphere in the central, the anterior, and the dorsal portion of that nucleus with the cells of the two most posterior (caudal) layers and those of the ventral layers remaining normal; (b) a complete absence of any undoubtedly degenerated nerve cells in the opposite external geniculate body; and (c) a complete absence of any degenerated nerve cells in the midbrain, especially in the superior colliculi.

In particular the left external geniculate body appeared in toto somewhat reduced in size in comparison with the right normal body. Of the left body the medioventral or internal and a portion of the lateroventral or external segment remained normal; of the most posterior (caudal) segment a portion also remained normal—at least the cells exhibit here less advanced degenerative changes than those of the undoubtedly degenerated segments. Roughly, the degenerated portions of the left external geniculate body comprised the intermediate or the macular segment and the greater portion of the lateral segment as far as the dorsal end of the nucleus (consider the segments as they usually appear on the frontal sections through the geniculate body, e.g., fig. 16). The boundary lines or lines of demarcation between the normal and degenerated segments of the cell layers are in the greater part remarkably sharp, in only few instances did the normal and the degenerated cells mingle for a short distance. It is noteworthy that the degenerated zones did not respect the cell layers but passed through two or more of the layers at the identical levels. Further the emphasis has to be put upon the fact that in the portions of the geniculate body which degenerated the process of degeneration was complete: no nerve cells—large, medium-sized, or small—could be found which could be regarded as normal or even less advanced in the degenerative process. On the contrary, in the normal segments none of the nerve cells showed definite signs of degeneration, or at any rate, they showed only slight changes.

In the opposite external geniculate body all nerve cells appeared perfectly normal, of the normal size, of normal angular configurations, and well stained.

In the ventral and ventro-lateral portion of the left pulvinar of the thalamus there was an almost complete degeneration of its nerve cells. This was very probably due to the damage of the parieto-occipital cortex outside the striate area proper. The rest of the thalamus and of the midbrain appeared to be normal.

Thus the present experiment revealed: (*a*) that only the external geniculate body of the same side degenerated when its striate area was destroyed, which means the non-existence of the hypothetical "fasciculus corporis callosi cruciatus"; (*b*) that all cells of the external geniculate body degenerated after the destruction of the corresponding striate area, which means the absence of intercalated nerve cells ("Schaltzellen" of Monakow) in that body; (*c*) that the destruction of the opercular striate area was followed by the degeneration of the macular segment of the external geniculate body; and (*d*) that the sparing of both lips and of the floor of the calcarine fissure in its anterior (oral) half was followed by the sparing of the lateral and medial segments of the external geniculate body and of its ventral layers containing large cells, layers corresponding with the "peripheral" portions of the hemiretinae including the monocular temporal crescent. (Compare Chapter XVI.)

EXPERIMENT V-E

In a young Java monkey the left occipital lobe was at first luxated and then with a few cuts quickly separated from the rest of the hemisphere by means of a Graefe's knife. The anterior portion of the calcarine fissure was removed subsequently by means of small scissors and a lancet.

Twenty-two days after the operation the animal was killed. There was found no open wound of the skin in the region of operation, no pus or inflammation beneath the skin or bone flap. The latter fitted exactly into the defect of the skull, the rows of small trephine holes having been already filled with a cartilaginous substance. The dura was found adherent to the left hemisphere, but only in the portion covering the defect. Macroscopically and microscopically the entire striate area of the left occipital lobe including its portion in the anterior half of the calcarine fissure (remaining normal in the preced-

ing experiment) was found to be absent. Other areas destroyed were: over the lateral face of the hemisphere the upper half of the area periparieta including its portion lining the sylvian sulcus—the lower third of that area remained normal—and the upper half of field 7. Over the inner face of the hemisphere the entire field 18 of Brod-

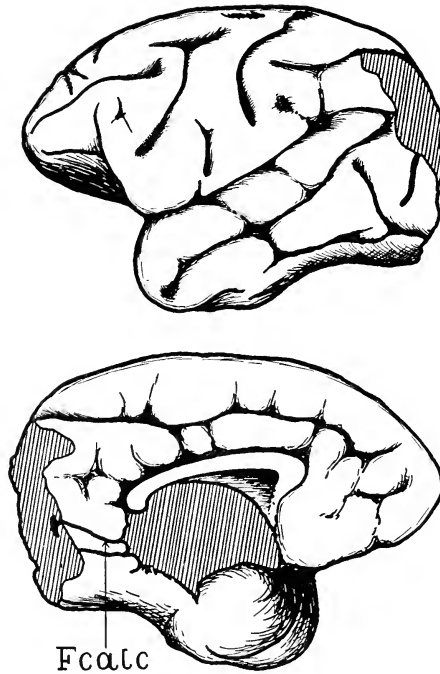


Fig. 20, Experiment V-E. External (upper figure) and internal (lower figure) faces of the monkey's hemisphere where the occipital lobe and the entire striate area including its portion sunk in the calcarine fissure (*Fcalc*) were removed. Areas shaded with lines represent cut surface of the occipital lobe, and after the removal of the betweenbrain. In this experiment the external geniculate body degenerated completely on the same side, the opposite body remained normal.

mann, the greater part of the dorsal half of field 19, and also the posterior portion of the lower half of the same field were destroyed. (Compare fig. 20.) The rest of the left hemisphere and the right hemisphere, as well as the remaining parts of the brain, showed a normal appearance.

The operation proved to be a shock for the animal, though somewhat less than in the foregoing case, and was followed by irregular respiration. One hour after the operation the monkey was found, however, already hanging high up on the wall of the cage. Eleven days after the operation no gross disturbance of the vision was apparent, so far as could be determined by simple observation of the behavior. It is doubtful, however, that the monkey saw anything that fell into the right halves of his visual fields. Two days later the animal did not seem to notice objects falling into the right halves of his visual fields, or at least he did not notice these with the same speed with which he noticed objects on his left side. When exploring the fur of his companion his visual behavior—the converging of both eyes in fixing and the visual control of fine movements of his fingers—appeared remarkably accurate. The next day the monkey with his left hand picked up the pieces of the apple and raisins falling into the left halves of his visual fields as far as the median sagittal plane. One day later the attempt was made in the company of Dr. H. Klüver to ascertain the presence or absence of a homonymous hemianopsia. The monkey was held by the extremities and by the neck in a fixed position by one person while the other person, standing behind, advanced the objects from the right or from the left side in such a way that the picture of these would fall upon either the right or the left halves of the retinae. The animal invariably moved his eyelids and turned his eyes toward the stimulus when it appeared on his left side, but the eyes and even the eyelids remained perfectly still when the object approached from the right side. There was a marked difference in the size of the pupils independent of the direction of the light. Three days later the monkey appeared to have some difficulties in exploring the heap of vegetables and fruit strewn over the floor of the cage: he slowly descended to the floor and at first cautiously surveyed the heap for a few seconds before choosing a morsel. In exploring he invariably used his left hand; he did not reach with his hand to the right over the midline (as did, for example, the monkey in the preceding case); at most he picked up the morsel that lay directly in front of him. A day later the monkey appeared fully recovered as far as his general behavior and condition were concerned; he was almost as vigorous and active as before the operation. Nevertheless, disturbance of the vision was the same, as before: ability to see only to the left, to grasp and take the morsels with his left hand, though afterwards when bringing the food to the mouth he could use well either of the hands separately

or both hands together. On the next day (last day of observation) the monkey took just the pieces of food lying to his left side, never those to his right. When picking up the morsels he behaved in a peculiar way, different from that of other monkeys, with a possible exception of a monkey with an isolated damage to the macular cortex of both sides (Experiment V-c). When descending to the floor of the cage where the pieces of food were scattered he was cautious, hesitating when looking straight forward, as if not recognizing sufficiently rapidly the various objects or morsels which were to his liking. The exclusive choosing of objects falling into the left halves of his visual fields was a well ascertained fact, as was also the preponderant use of his left hand. Only occasionally did he pick up objects with his right hand. In contradistinction to this he used his right hand very well in bringing food to the mouth, although he generally used both hands for this purpose. It was remarkable that even during a prolonged observation (the last day about three hours) the objects to the right were persistently left out of consideration. Another interesting feature was that, though he made no proper circus movements—that is more or less rapid movements around his own axis—when he sometimes slowly explored the rubbish covering the floor of the cage wherein various food particles lay scattered, he seemed to “follow” the functioning halves of his visual fields, in this case to the left, in such a way that in the course of one or of several minutes he described one-half or even one complete circle counter-clockwise in direction. A similar movement to the right in a sense opposite to the dial movement was never observed. Further observation shows that when the monkey used both hands, as in exploring the fur of his companion, the right hand was used in a more passive, accessory way. In picking up the “lice” or dandruff he seemed more slow than the animals with normal sight; he gazed every time for a while at the object before he actually “found” it. He seemed to have difficulties either in fixing, or in recognizing and identifying the objects, though this function appeared to be impaired rather in degree than in quality. The same disturbance was apparent when the monkey tried to take one of the peanuts from its shell. When he saw the edible nut he was quasi-puzzled, and then after a few seconds when he realized its meaning, he carried it to his mouth (the other nut, perhaps unseen or unrecognized, fell to the floor). The left pupil immediately after deep narcosis and after death appeared somewhat smaller.

From the above description it is fairly certain that in this experiment a complete homonymous hemianopsia to the right was produced by the complete destruction of the striate area of the left side.

A careful study of an uninterrupted series through both geniculate bodies, the thalamus, and the anterior portion of the midbrain, well stained with thionine blue according to Nissl's method revealed: (a) a complete degeneration of all nerve cells of the entire external geniculate body ipsilateral with the destroyed striate area (left), (b) a complete preservation of all nerve cells of the entire external geniculate body opposite to the side of the destroyed striate area (right), and (c) a complete absence of any changes of the cells of the midbrain, especially of the superior colliculi.

In particular, the left external geniculate body appeared reduced in size about one-fourth in comparison with the normal body of the right side. The individual fiber and cell layers of the left-sided body appeared also considerably reduced in thickness, their outlines blurred and indistinct, their nerve cells, not excluding the large elements of the ventral layers, exhibiting extensive degenerative changes notably the reduction in size and the poor staining. Not even individual cells remained normal, not to mention a complete absence of normal segments of cell layers. Only a few scattered cells were found to be stained somewhat better, but even these show marks of degeneration. The emphasis has to be put upon the fact that all the large cells of the ventral layers, which in the preceding experiment remained normal, degenerated completely in the present experiment. On the contrary the corpus (griseum) praegeniculatum of the left side, as well as the internal geniculate body of the same side preserved its normal appearance.

The external geniculate body of the side opposite the injured striate area (right) remained perfectly normal in all its parts including its intermediate macular segment. There are neither degenerated zones in it nor individual scattered degenerated nerve cells.

Likewise no degenerated nerve cells were found in the midbrain, particularly in the superior colliculi, though a portion of the pulvinar degenerated (due to the damage of the parieto-occipital cortex).

The present experiment demonstrated that: (a) the external geniculate body degenerated completely when the striate area of the same side was destroyed completely, (b) the external body remained fully preserved although its opposite striate area was completely destroyed, (c) no cells in the external geniculate body remained

normal when its ipsilateral striate area was destroyed, and (*d*) no cells in the midbrain, notably in the superior colliculus, degenerated after the destruction of the striate area. All this implies the absence of any other bypaths which might originate from the external geniculate body, except the visual radiation which is ipsilateral or uncrossed, and terminates in the striate area; also there are no intercalated nerve cells in the external geniculate body—all cells of that body irrespective of size and location send their fibers to the striate area. The midbrain does not send fibers to the occipital lobe. (Compare Chapter XVI.)

CHAPTER XV

CORTICAL TERMINATIONS OF THE VISUAL AFFERENT
FIBERS (FINDINGS)

As regards the finer details and the modes of intracortical terminations of the afferent visual fibers, as far as such information can be secured by Marchi's method, the following facts deserve to be mentioned.

In the fissura calcarina, where these details were particularly studied, the afferent visual fibers occupy, as mentioned before, the zone of the subcortical white substance close beneath the striate cortex (figs. 57, 65, 72, 73, 75, 76). From this zone they gradually penetrate into the cortex mostly in slightly curved arches, sometimes also in sharp turns. Arriving in the cortex (fig 65), they ascend through the lower cortical strata directly or more obliquely upward toward the stripe of Gennari or *Vieq d'Azyr* represented in the figure 65 by the uppermost of the three horizontal striae (this figure as well as figs. 57, 72, 73, 75, 76, show at the points marked with arrows the abrupt cessation of all the mentioned striae, indicating the boundary of the striate cortex).

Within the striate cortex the exogenous visual fibers, however, seldom lie parallel to the actual "radiated" bundles and for the most part do not correspond with them. (Compare an identical observation with regard to the thalamo-cortical fibers in the somatic sensory cortex, Chapter VII, and figs. 58-64.) Some of the exogenous visual fibers reach the stria Gennari or *Vieq d'Azyr* in a more irregular way. A few traverse, as horizontal or oblique fibers, longer or shorter stretches within the lower cortical strata immediately adjacent to the white subcortical substance. Within the lower cortical strata, the sixth and the fifth layers of Brodmann, the ninth, the eighth, the seventh, and the sixth layers of Ramón y Cajal, the afferent visual fibers are mostly coarse, although less than when still within the white subcortical substance.

In my preparations degenerated fibers, gradually decreasing in size and number, have been seen to ascend toward the surface of the cortex as far upward as the 4-b cell layer of Brodmann containing the stripe of Gennari-*Vieq d'Azyr*, the fourth cell layer of Ramón y Cajal, indi-

cated by the uppermost stripe in figure 65 (this stripe, being also the broadest, corresponds to the entire 4-*b* fiber layer of Vogt [1919, fig. 34], the intermediate stripe being Vogt's 5-*b* fiber layer, the ventral stripe corresponding to Vogt's 6*ba* fiber layer). Farther up dorsally within the layer 4-*a* of Brodmann (see Brodmann, 1909, fig. 69) approximately corresponding with the lower portion of Ramón y Cajal's third cell layer, only a few blackened particles and dots were seen. The upper layers of the striate cortex: the first, the second, and the third cell layer of Brodmann, but almost, thus, the upper portion of the fourth cell layer of Brodmann (his 4-*a*)—, accordingly, do not contain, in the present experiments, any disintegrated medullary fibers. The fourth cell layer of the striate area, according to Brodmann's division, corresponds with the following layers of Ramón y Cajal: with the lower portion of the layer of medium sized pyramidal cells (ventral portion of the third cell layer of Ramón y Cajal, lamina granularis interna superficialis or the 4-*a* layer of Brodmann), with the layer of large asteriform cells (fourth layer of Ramón y Cajal, lamina granularis interna intermedia or the 4-*b* layer of Brodmann), with the layer of small asteriform cells (fifth layer of Ramón y Cajal, a little less than the lamina granularis interna profunda or the 4-*c* layer of Brodmann), and with the uppermost portion of Ramón y Cajal's sixth layer composed of small pyramidal cells discharging an ascending axis cylinder.

According to the present investigations it is the lower portion of the fourth layer of Brodmann (4-*b* and 4-*c*) or approximately the fourth and the fifth layers of Ramón y Cajal, the main granular cell layer of the striate cortex and the stripe Gennari-Vicq d'Azyr, and also the layers situated ventrally, Brodmann's fifth and sixth layer, Ramón y Cajal's sixth, seventh, eighth, and ninth layers, which contain numerous degenerated afferent visual fibers.

When comparing carefully the present findings regarding the relation of the afferent visual fibers to the various cell and fiber layers of the striate cortex with Ramón y Cajal's description of the terminations of exogenous afferent fibers in the human striate area found by means of Golgi's silver impregnation (compare my fig. 65 with fig. 390, p. 613, and especially with fig. 391, p. 615 in Ramón y Cajal's work, 1909-11, vol. 2), it becomes apparent that the uppermost layers which still contain afferent fibers in the present experiments are the fourth and the fifth layers and also the upper portion of the sixth layer of Ramón y Cajal or approximately the 4-*b* and 4-*c* layer of Brodmann. It

is especially 4-*c* layer of Brodmann, Ramón y Cajal's fifth layer, which contains a great number though of only fine and very fine blackened fibers and granules (while in the lower layers the fibers and dots are coarser). In these layers, according to Ramón y Cajal, afferent visual fibers disperse into terminal ramifications, contributing partly to the formation of the external stripe of Baillarger or the stria Gennari or Vieq d'Azyr. It is the fifth layer of Ramón y Cajal where the densest plexus of the exogenous fiber terminations is found (in Ramón y Cajal's fig. 391 marked with *B*). This layer corresponds, on the whole, with Brodmann's lamina granularis interna profunda (4-*c*) containing numberless small cells or granules, situated immediately beneath the layer of the large asteriform cells. Yet the latter layer, fourth layer of Ramón y Cajal (in his fig. 391 marked with *A*), Brodmann's 4-*b* layer, also receives, according to Ramón y Cajal, numerous terminal branches of afferent visual fibers, although the fiber plexus is here less dense than in Ramón y Cajal's fifth layer, Brodmann's 4-*c* layer.

In my preparations the zone of Gennari's stripe, 4-*b* layer of Vogt, Brodmann's 4-*b* layer, contains accordingly only a few and only fine blackened granules, the latter increasing in number and in size toward the ventral layers (Brodmann's 4-*c*, fifth and sixth layers). The slight discrepancy between Ramón y Cajal's findings and mine can easily be explained by the loss or at least the considerable reduction of myelin sheaths of the ultimate rami of the afferent visual fibers after they enter the zone of the stripe of Gennari or Vieq d'Azyr. It is, however, remarkable that in our preparations the 4-*c* layer of Brodmann, Ramón y Cajal's fifth layer, is the place of termination of numerous fine myelinated fibers, exactly the layer which, according to Ramón y Cajal, contains the densest meshwork of ultimate branches, although fine degenerated fibers also ascend unquestionably in a moderate number into the stria Gennari-Vieq d'Azyr.

Ramón y Cajal also found the upper strata above the fourth layer, layers 1, 2, 3, and 4-*a* of Brodmann, to be reached only by rare delicate branches ascending from the dense meshwork below. He therefore regards the upper strata (his first, second and third layers) as hardly being in direct relation with the bulk of the afferent visual fibers. The lower strata, the sixth, seventh, eighth, and ninth layers of Ramón y Cajal, the fifth and the sixth layers of Brodmann, on the contrary receive a certain although also a small number of fine branches, while the coarse fibers here are the ones that merely pass toward the fourth layer of Brodmann, fourth and fifth layers of Ramón y Cajal (according to Ramón y Cajal).

From the above description of the results of the present study of the minute relations of the afferent visual fibers to the various cell and fiber layers of the visual cortex in the brain of the monkey, it is apparent that they stand in all essential points and even in most details in full agreement with those found by means of a different method by Ramón y Cajal in the brain of man. But the present investigations would appear to have further importance in as much as they have, for the first time, clearly demonstrated that in the brain of primates the visual fibers originating from the subcortical nuclei are identical with certain intracortical fiber elements of the striate cortex. The present studies show that a part of the "basal meshwork" in the lower cortical strata ("Grundfaserfilz" of Vogt, 1919, his fig. 34; see also Maass), especially the stronger fibers in that meshwork which often have an irregular oblique course, are nothing other than incoming afferent visual fibers originating in the external geniculate body. (Compare a similar observation on the termination of the somatosensory thalamo-cortical fibers, Chapter VII.) Thus our work furnishes the final proof for Ramón y Cajal's opinion of the nature of the coarse exogenous fibers of the striate cortex found and considered by him to be terminations of the afferent visual fibers, a supposition, which although probable, remained until now without definite confirmation, due to the inability of Golgi's method to demonstrate long stretches of fibers. The present experiments also show an essentially identical arrangement of the intracortical afferent visual fibers both in higher and in lower mammals (see Ramón y Cajal, 1922 and 1923, and my previous investigations on the termination of afferent visual fibers in the brain of the cat, 1927, fig. 36). It seems proper to claim for the present experiments, that they have fulfilled the requirement demanded long ago by Monakow (1914, p. 353) as regards the experimental verification of the visual radiation in primates, though the results turn out to be very different from Monakow's view of the extension of the visual projection cortex and of the internal organization of the visual radiation, and, in fact, contrary to most of his views on the organization and function of the visual apparatus. (See Chapter XVI.)

CHAPTER XVI

VISUAL SYSTEM (DISCUSSION)

After the preceding detailed description of the conditions of the visual system in the present experiments I would give here firstly, a brief summary of the results deduced therefrom, secondly, a discussion of the arguments in support of my statements, thirdly, a consideration of a few outstanding physiological and pathological problems of vision, and finally, a formulation of further problems relating to this system, as they appear in the light of the present results.

The present experiments show that:

(1) The external geniculate body of the between-brain must be recognized at present as the only and the exclusive origin of the visual radiation in primates.

(2) There exists only one single direct afferent visual path from the subcortical region to the cerebral cortex. (Nothing positive is known of indirect visual paths.) It is the fiber system originating from the external geniculate body. That external geniculo-cortical radiation forms a strong fiber lamina or layer identical with the "primäre Sehstrahlung" of Flechsig, with the stratum sagittale laterale of H. Sachs, a portion of which was called by Burdach, Wernicke, and Monakow "fasciculus longitudinalis inferior" of the parieto-occipital and temporal lobes. However, other fibers: efferent, callosal, and associational, mix with the afferent visual fibers. Stratum sagittale internum, "sekundäre Sehstrahlung" of Flechsig, is an efferent fiber system. The tapetum is composed exclusively of callosal fibers.

(3) The cortical region where the visual path terminates is a single, definite, and sharply delimited area which is identical with the area striata of G. E. Smith, field 17 of Brodmann, or area OC of Economo-Koskinas distinguished by the strong intracortical fiber layer, the stripe of Gennari or Vieq d'Azvr (fig. 21). No other areas of the cerebral cortex receive afferent visual fibers.

(4) The central visual path above the external geniculate body is strictly unilateral. No evidence exists of a partial decussation of its fibers through the corpus callosum ("fasciculus corporis callosi cruciatus"). The only spot, therefore, where the visual path undergoes a partial decussation is below the between-brain in the optic chiasm.

(5) The fibers of the visual radiation are, on the whole, finer than the somatic sensory (thalamo-cortical) fibers. Most of the visual fibers are of medium size, only a small number having a large caliber. The coarse visual fibers almost exclusively enter the fissura calcarina and the pole of the occipital lobe, the thin or medium sized fibers enter the pole of the occipital lobe and the occipital operculum. The visual fibers, however, exceed in caliber the association and callosal fibers of the striate area and of the occipital lobe generally.

(6) The visual radiation is composed of fibers grouped into fiber bundles arranged, on the whole, in parallel fashion. Each fiber bundle originates in a definite small segment of the external geniculate body and terminates in a definite small segment of the striate area.

(7) The visual radiation or the external sagittal layer of the parieto-occipital lobe can be subdivided into three anatomical-functional portions discernible on cross-sections perpendicular to the long axis of the hemisphere: (a) the dorsal horizontal branch, (b) the ventral horizontal branch, and (c) the vertical or the perpendicular branch connecting both horizontal branches. The dorsal horizontal branch is composed of fibers originating in primates from the medial (internal) segment of the external geniculate body close to the thalamus which corresponds with the upper extramacular segments of both homonymous hemiretinae, including the upper monocular portion of the crossed retina. This branch supplies the striate cortex of the upper (dorsal) lip of the fissura calcarina, with the most dorso-medio-anterior bundle, the dorsal "boundary bundle" of the radiation, supplying the most internal longitudinal "boundary segment" of the upper lip, and with the successive lateral bundles supplying the more lateral and somewhat caudal segments closer to the floor of the calcarine fissure and to the axis of the striate area. The ventral horizontal branch is composed of fibers originating from the lateral (external) segment of the external geniculate body close to the lentiforme nucleus, corresponding with the lower extramacular quadrants of both homonymous hemiretinae, including the lower monocular portion of the crossed retina. It supplies the striate cortex of the lower (ventral) lip of the fissura calcarina. The narrow zones of the striata area supplied here are probably similarly arranged longitudinally as are those in the upper lip, but in reverse order, with the most medial zones being supplied by the most ventro-medio-anterior bundle, and so forth. The perpendicular (intermediate) branch of the visual radiation is composed of fibers originating from the large inter-

mediate segment of the external geniculate body, which is situated between both internal and external segments of that body. This intermediate segment corresponds to both dorsal and ventral quadrants of both homonymous hemimaculae. The vertical branch represents a considerable portion, probably more than half, of the visual radiation. It supplies the striate cortex covering the pole of the occipital lobe, and in the monkey, as far as the striate cortex extends, the external face of the occipital lobe or the so-called operculum occipitale. The vertical branch represents in its upper half, near the dorsal horizontal branch, the upper quadrants of both homonymous hemimaculae; in its ventral half, near the ventral horizontal branch, the lower quadrants of both homonymous hemimaculae (fig. 22).

(8) In view of the above statements and the results of pathological and experimental studies of Rönne (1914) and of Brouwer-Zeeman (1926), the following conclusions as to the projection of the retina upon the cortex in primates and in man must be made (fig. 23).

(a) The upper extramacular quadrants of both homonymous hemiretinae (lower quadrants of the homonymous halves of the visual fields with exclusion of the macular portion), together with the upper half of the monocular portion of the crossed retina (lower half of the crossed temporal crescent) are projected upon the upper lip of the fissura calcarina (in man, anterior portion of that lip).

(b) The lower extramacular quadrants of both homonymous hemiretinae (upper quadrants of the homonymous halves of the visual fields with exclusion of the macular portion), together with the lower half of the monocular portion of the crossed retina (upper half of the crossed temporal crescent) are projected upon the lower lip of the fissura calcarina (in man, anterior portion of that lip).

(c) The projection zone of the monocular temporal crescent occupies the anterior portion of the calcarine striate area, being its most "peripheral" zone (in the monkey in both lips).

(d) Homonymous halves of both maculae luteae and of the fovea centralis are projected upon the pole of the occipital lobe, in the monkey behind the ascending and descending branches of the fissura calcarina, and upon the external face of the occipital lobe, the occipital operculum, as far as the striate cortex extends. The upper half of the polar and the opercular striate cortex represents upper quadrants of both homonymous halves of the maculae (lower homonymous quadrants of the macular portion of the visual fields); the lower polar and opercular half represents the lower quadrants of both homonymous

halves of the maculae (upper homonymous quadrants of the macular portion of the visual fields). The fovea centralis in particular is projected upon a middle zone stretching across the pole and, in the monkey, across the operculum of the occipital lobe fairly horizontally. In the monkey the foveal projection is probably close to the shallow impression, the external calcarine sulcus or superior occipital sulcus, dividing the operculum occipitale into an upper and a lower half.

(e) The horizontal meridian, dividing the upper homonymous extramacular quadrants of both hemiretinae and of the crossed monocular portion and corresponding portions of the visual fields from lower quadrants, extends in a longitudinal sense, along the bottom of the fissura calcarina. Its continuation around the occipital pole and, in the monkey, over the occipital operculum approximately toward the midpoint of the sulcus simialis, corresponds with the horizontal meridian dividing the upper and lower quadrants of both homonymous hemimaculae. The vertical line dividing both homonymous halves of the visual fields of both eyes and passing through the points of fixation is represented by the posterior boundary of the striate area; in the monkey it stretches in a fairly parallel way along the sulcus simialis. The points of fixation must, therefore, correspond with a central point of that boundary. The dividing line between the macular and extramacular cortex probably has the shape of a sickle with both its horns inclined occipitalward embracing the macular portion of the striate area in front along both ascending and descending branches of the fissura calcarina (in the monkey). Since both horns of the extramacular cortex terminate in sharply extended wedges, the macular cortex in its posterior, and in the monkey in its opercular portion, is not completely surrounded by the extramacular cortex.

(9) The bilateral or the double cortical representation of each total macula, with each and all of its receptor elements connected with both hemispheres, has no anatomical foundation. The individual macular elements are represented only in one hemisphere. But each half of each macula is projected upon another hemisphere. In other words, each macular cortex represents homonymous halves of both maculae.

(10) The entire striate area receives everywhere afferent visual fibers. There exist no visible gaps (small cortical zones without an afferent fiber supply) which might separate small supplied cortical islets. The number of afferent visual fibers per cortical square unit appears to be larger in the occipital pole and in the occipital operculum than in the calcarine fissure (in the monkey). The coarse exogenous

fibers of the visual cortex entering more or less obliquely the lower strata and terminating in the zone of the stripe of Gennari or Vieq d'Azyr, described by Ramón y Cajal, are afferent visual fibers originating in the external geniculate body of the same hemisphere.

(11) The small segments of the visual cortex supplied by individual bundles of the visual radiation have sharp limits and definite form. In different portions of the striate area their shape is different: long narrow triangular strips in the fissura calcarina arranged longitudinally, but more condensed triangles in the occipital operculum and over the occipital pole. The afferent fiber bundles of each of these small cortical triangles are strictly isolated one from another. Each triangle of the visual cortex gets its own bundle independently from the neighboring triangle. There does not, accordingly, exist an overlapping of these small zones, a mingling of their respective bundles, or even a "diffuse" termination of individual bundles of the visual radiation in extensive portions of the visual cortex. Neighboring triangles are supplied by neighboring fascicles of the visual radiation.

(12) The entire afferent visual system from its beginning in the peripheral organ (retina) to its termination in the cerebral cortex (striate area) is composed of individual receptor and conductor units. These structural and functional units are strictly arranged according to the "spatial principle" on the one hand, and according to the "principle of neighborhood" on the other. Each area striata is in some sense a faithful copy of both homonymous halves of both retinae. There exists a full preservation of "spatial relations" in the visual cortex as it exists in the retina, though the absolute shape of the "cortical hemiretina" is somewhat changed in consequence of the slight mutual displacement of neighboring units or segments.

(13) All visual impulses whatever their special form or quality may be, and regardless of their ultimate destination, so far as they reach the cortex of the forebrain, first go to the striate area from which they are distributed to other regions of the same and the opposite hemisphere.

(14) Since there exists a fixed arrangement of functionally different bundles or segments of the visual radiation (present experiments) as well as of the peripheral portion of the visual system (Rönne, Brouwer-Zeeman), which means a fixed projection of definite retinal quadrants upon definite portions of the visual cortex, symmetrical in both hemispheres, the injuries of the visual system will produce definite symptoms depending on the location and the extent of the injury.

Since each of the constituent structures of the afferent visual system and of the visual cortex has its own function, its destruction will be followed by an irreparable and lasting loss of that particular function. The replacement or compensation of the lost function must be achieved by what can be called a more economic utilization of the parts remaining undamaged.

1. VISUAL RADIATION; ITS SUBCORTICAL ORIGIN, ITS COURSE, AND ITS CORTICAL TERMINATION

In passing to the discussion of arguments for the above statements, to remain on firm ground, the organization of the peripheral portion of the visual system must first be considered. Here, naturally, we must rely upon the fundamental studies of Brouwer and his collaborators. As is evident from Brouwer-Zeeman's, Minkowski's, and Overbosch's experiments, all peripheral optic fibers originating in the retina terminate either in the external geniculate body and in the corpus praegeniculatum, or in the superior colliculus of the midbrain. This alone excludes the thalamus proper from the rank of a subcortical visual center. Neither does there exist, as explained previously, other evidence which will withstand a critical examination, to support the opinion of a threefold subcortical origin of the visual radiation (Monakow), in man and other primates. The present experiments are also clearly detrimental to that view since it was found that the brachium of the superior colliculus degenerates in the cortico-fugal sense, from the parieto-occipital cortex to the colliculus (figs. 36, 96), and no cells of the colliculi degenerated after the destruction of the striate area (Experiment V-D and V-E). On the other hand, no ascending fibers were found which might connect the pulvinar with the occipital lobe. Equally the thalamus proper, its dorso-lateral and its ventro-lateral nucleus, must be excluded from the direct cortico-petal visual path. Since all evidence points to the external geniculate body as the only and exclusive internuncial station of the cortico-petal visual fiber system, that nucleus will therefore be considered exclusively in all further discussions.¹

The visual radiation with its exclusive origin in the external geniculate body forms, on the whole, a single, compact, and well defined fiber system. It is composed of fine and medium sized fibers, preponderantly, and of coarser fibers. The coarser fibers are scattered

¹ The corpus or griseum praegeniculatum must also be excluded.

more in the external half of the external sagittal layer and in both horizontal branches. The visual radiation is identical with the fiber lamina called by descriptive anatomy the external sagittal layer of the parieto-occipital lobes (H. Sachs). This fiber lamina on cross-sections through the hemisphere is shaped like a horse-shoe with its concavity facing inward and embracing the internal sagittal layer, the tapetum, the posterior horn of the lateral ventricle, and the fissura calcarina (figs. 39, 55, 95). It can roughly be subdivided into an upper and a lower horizontal branch, each of them entering its corresponding lip of the fissura calcarina, and into a vertical or perpendicular branch linking together both horizontal branches, and reaching the occipital pole.

The fibers of the external sagittal stratum have, on the whole, a longitudinal oral-caudal course. They are grouped into bundles which, in parallel arrangement, run their entire course occipitalward. The dorsal and ventral fiber bundles very gradually accomplish a spiral turn of ninety degrees or more around the lateral ventricle. Individual fibers and bundles, especially those extremely medial in the upper and lower horizontal branches, must twist considerably more. Both upper and lower branches describe a spiral in the reverse sense (fig. 22). The bundles of the vertical branch have a straighter course toward the occipital pole. The totality of the fibers of the visual radiation form a fiber "fan" with handle near the external geniculate body, its "ribs" gradually but not equally diverging from one another and radiating toward the cortex. The visual or external geniculocortical radiation can be looked upon as a separate, specialized portion of the huge diencephalo-cortical afferent fiber system. Near its origin (*cgl*) it is close to the somatic sensory and auditory paths (*sr* and *ar* in figs. 30-34, 51, 52); toward the cortex it diverges from these two paths. However, it is accompanied for a considerable distance by the posterior bundles of the somatic sensory (thalamocortical) fibers; the dorsal bundles of the visual path which form the upper horizontal branch of the external sagittal layer are closest to the somatic sensory path (figs. 52-55, 67-69, 71). The intermediate and ventral bundles forming the perpendicular and ventral horizontal branch, especially the latter, are near their origin beneath the temporal lobe close to the auditory path. Although the visual radiation forms a well defined fiber system, it is penetrated by other systems: by ascending and descending callosal fibers, by association fibers (figs. 87-94), and by corticofugal fibers descending from the occipito-

parietal lobes (lower degenerated bundles *tet* in fig. 69 and especially figs. 95, 96). These latter form in the parietal lobe the internal sagittal layer of Gratiolet's radiation, that layer hardly existing in the occipital lobe (in the monkey). A number of efferent fibers, however, descend also in the external sagittal layer itself (fig. 95). The tapetum which is quite poorly developed in the occipital lobe (better in the parietal lobe), is a callosal system (figs. 37, 38, 67, 68, 70, 95).

As to the possibility of a partial decussation of the fibers of the visual radiation through the splenium of the corpus callosum, a possibility accepted by some investigators (Heine, Lenz, Niessl von Mayendorf, R. A. Pfeifer, 1925; Foerster, 1929, Foerster-Penfield) to explain the preservation of macular or "central" vision in cases of the hemianopsia of a central origin, no evidence whatsoever has been found in the present experiments which would favor such an hypothesis (see also Flechsig, 1927, pp. 93, 94). The present experiments decidedly demonstrate the unilateral character of the central visual path from its beginning in the external geniculate body to its termination in the striate area of the same hemisphere.² This observation is the counterpart of the observation of a similar unilateral character found in the present experiments for the other two main afferent paths of the cerebral cortex (see: Somatic Sensory System, and Auditory System). In so far as the transmission of peripheral impulses to the cerebral cortex alone is concerned, all three afferent paths: the somatic sensory, the auditory, and the visual, represent in their central portion above their diencephalic origin strictly unilateral, non-decussating fiber systems. (The same was found in other experiments as valid for the intrahemispheric portion of the pyramidal fibers since no cortico-bulbar and cortico-spinal fibers decussating in the corpus callosum, as claimed by some investigators, were seen.) Where there is a partial or a total decussation of the three main afferent paths, this is accomplished below the level of the diencephalon or in the latter. In the optic system: the chiasm; in the auditory system: the corpus trapezoideum and perhaps the midbrain; in the somatic sensory system: the spinal cord, the brain stem, and perhaps also the between-brain. The sparing of macular or "central" vision is due to special anatomical peculiarities of the visual radiation which will be dealt with later.

² See remark on p. 180.

Just as one single definite central visual paths exists, so also there is but one terminal cortical area, primary or projectional visual cortical area. Although in the preceding experiments various portions of the visual radiation were interrupted and degenerated, it has been found that visual fibers enter exclusively the striate area of Elliot

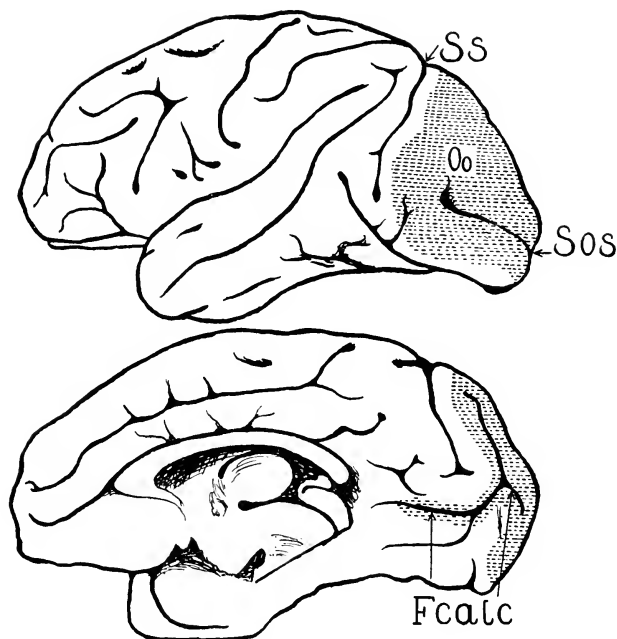


Fig. 21. A diagram showing the position and the extent of the visual projection cortex in the brain of the monkey as determined in the present investigation. This area is identical with the area striata of Elliot Smith or Brodmann's field 17 (compare with fig. 7) both on the lateral face (upper figure) and on the medial face of the hemisphere (lower figure). In the monkey the striate area along the undivided horizontal branch of the calcarine fissure (*Fcalc*) remains hidden in the fissure, emerging on the surface only along the ascending and descending branches of that fissure. Over the convex face of the occipital lobe in the monkey the striate area extends over the greater part of the occipital operculum (*Oo*) behind the simian sulcus (*Ss*) and is divided into two unequal portions, an upper and a lower, by the superior occipital or external calcarine sulcus (*Sos*).

Smith or field 17 of Brodmann, corresponding with area OC of Economo-Koskinas. No afferent fibers which could be called visual were seen to enter any other area of the occipital, much less the

parietal lobe. Thus no such fibers enter the area peri-parastriata of Elliot Smith, the areas 18 and 19 of Brodmann, the areas OA and OB of Economo-Koskinas, or even their area, OB_y, called *limes parastriatus gigantopyramidalis*. (The somewhat different results as regards the latter area obtained previously in my experiments with cats, 1927, are probably due to the difficulties of an accurate delimitation of that area in the cat; on the contrary in the monkey, the limits of the stria Gennari or *Vieq d'Azyr* can everywhere be easily determined; see paragraph 6 in this chapter.) No matter how the present experiments varied and what portion of the visual radiation may have happened to degenerate, the cortex receiving degenerated fibers always coincided with a smaller or larger portion of the striate area. In all cases the limits of the striate cortex were strictly observed (figs. 13, 40-42, 55-57, 65, 69, 71-76). It is, therefore, safe to conclude that the visual projection cortex and the striate area are fully identical. Experiment II appears especially valuable in this respect. Here, although the subcortical injury is larger than in any of the remaining three experiments, because of greater distance of the injury from the occipital lobe and a favorable position of the injury, no degenerated association or callosal fibers obscured the picture. This experiment, and the remaining four scarcely leave a doubt as to the absence of any direct or even indirect connections between the subcortical visual stations and the cerebral cortex save by means of the external geniculo-cortical radiation to the striate area. It appears, therefore, that no reasonable arguments can be advanced against a definite settlement of the long continued dispute as to the question of whether the central visual path does reach a "wide" region of the occipital and perhaps also of the parietal lobe, or whether, on the contrary, it terminates in a comparatively small, sharply delimited cortical area of the occipital lobe. The conception of a "diffuse" projection of the retina upon a wide region of the cerebral cortex or even upon several different and perhaps widely distant regions has no anatomical foundation. The opponents of a single well delimited visual cortical projection area must reconcile themselves with this conception by realizing that there is sufficient room in the striate area for the projection of the entire retina and for the reception of all impulses transmitted from the retina to the cerebral cortex. The special emphasis here put upon the existence of a single, definite visual projection "center" as resulting from the present experiments does not appear superfluous. The fiction of a diffuse or

perhaps multilocular cortical projection of the retina seems apparently not to have lost all its adherents even in modern times. Because of the lack of convincing anatomical arguments old decentralistic objections are every now and then brought forward against attempts to explain rationally the visual mechanisms and their function.

2. INTERNAL ORGANIZATION OF THE VISUAL RADIATION. PROJECTION OF THE RETINA UPON THE VISUAL RADIATION

After having shown in a definite way, as it appears, that there exists only one, single subcortical visual nucleus, the external geniculate body, which gives rise to one, single, definite central visual path terminating in one, single, sharply delimited cortical region, the striate area; further details must be discussed, that is, the origin, the course, and the termination of particular bundles or segments of the visual radiation, and their particular functional significance. In this way we may expect to determine the exact projection of the retina upon the visual projection cortex.

Here we must again turn to the investigations of Rönne and particularly to the experiments of Brouwer and his co-workers since they served as a starting point and as an indispensable preliminary foundation for the present investigations. The results of these studies can be summarized as follows: both superior quadrants of the extramaeular homonymous retinae are projected upon the internal segment of the external geniculate body, the inferior quadrants upon the external segment, the macula upon the intermediate segment of that body.

In the present experiments it was found that bundles which form the dorsal portion of the visual radiation originate from the internal segment of the external geniculate body (Experiments II and III; this is also clear from Experiment V-B). By forming the dorsal horizontal branch of the external sagittal layer, they enter the upper lip of the fissura calcarina, approximately as far as the bottom of that fissure (figs. 55-57, 69-74). This portion of the visual radiation, as said before, neighboring at its origin the dorso-caudal somato-sensory (thalamo-cortical) fibers (figs. 52-55, 67-69, 71) which ascend toward the upper parietal region, also ascends at first in a fairly perpendicular though somewhat caudally inclined course before turning occipitalward (figs. 52-54). At the same time these dorsal bundles gradually describe a spiral turn around and above the posterior horn of the

lateral ventricle and finally turn down into the upper lip of the fissura calcarina where they again turn partly oralward (figs. 75, 76). In other words, the dorsal portion of the visual radiation has its own course, remains dorsal during almost its entire course, and does not mix with other portions of the radiation. Neither does it come closer to the ventral lip of the calcarine fissure, as alleged by some investigators, nor does it pass through the thin fiber layer covering the calcar

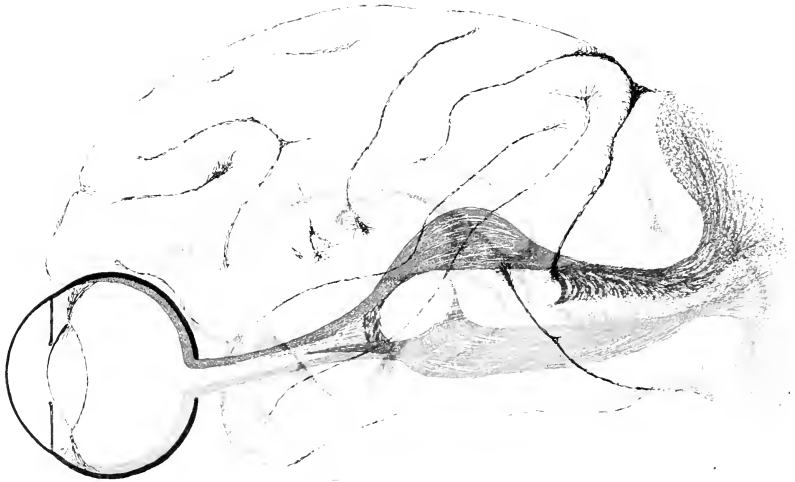


Fig. 22. A scheme to show the course and the arrangement of the entire afferent visual path from its beginning in the retina of the eye (left in the figure) to its termination in the occipital lobe (right in the figure). Right hemisphere of the brain of *Macacus* viewed from the internal side and imagined transparent. Contours of the hemisphere, of the convolutions and furrows, and of the eye-bulb grey or black; in the retina, in the optic nerve and optic tract, in the external geniculate body and in the visual radiation green color corresponds to the lower extramacular quadrants, yellow to the lower macular quadrants, blue to the upper extramacular quadrants, pink to the upper macular quadrants. In the external geniculate body and in the visual radiation the relative position of various bundles corresponds to their actual position as found in the present investigations (combined with those of Brouwer-Zeeman). Both upper and lower extramacular fibers enter upper and lower lip of the calcarine fissure respectively; macular fibers interposed between both extramacular bundles enter the pole of the occipital lobe and the operculum occipitale. (For explanation see Chapter XVI, 2, and Chapter XVII.)

avis to reach in this way the lower lip. Its fibers in part only, in so far as they are destined for the deeper portions of the upper lip closer to the bottom of the calcarine fissure, penetrate into the calcar avis; yet they penetrate only from above (figs. 70, 72, 75, 76). Because of

the spiral course neither the upper nor the lower horizontal branch can be seen in its entire length in a single section or even in a few closely neighboring sections.³

Accordingly, we must look on the dorsal horizontal branch of the visual radiation as transmitting impulses from the superior extramacular quadrants of the homonymous halves of both retinae to the upper lip of the fissura calcarine (figs. 22, 23).

The next portion of the visual radiation, forming the intermediate perpendicular branch of the external sagittal layer, has been traced in the present experiments up to the pole of the occipital lobe and to the occipital operculum (Experiment I and especially V-A, and partly Experiment IV). Although this portion of the radiation has not been interrupted at its origin, it is fairly safe to regard it as not originating from the internal but from the next laterally situated large intermediate segment of the external geniculate body, which segment, according to Rönne (1914) and Brouwer-Zeeman (1926), receives macular fibers from the retinae. It is this and the lateral segment of the external geniculate body as well as their bundles of the radiation which remained undamaged in Experiments II and III where the perpendicular and the lower horizontal branch of the external sagittal layer remained normal. The question which could be asked here is whether the perpendicular branch of the external sagittal layer does not also originate from the lateral segment of the external geniculate body. Knowing, however, on the one hand, from Rönne's and especially from Brouwer's studies, the orderly sequence in the arrangement of the segments of the external geniculate body, with the macular segment being placed between both "peripheral" segments, and on the other hand, the parallel arrangement of the bundles of the visual radiation, the only possible origin of the perpendicular branch of the visual radiation in the existing order or sequence of the segments is the intermediate macular segment of the external geniculate body. This is also supported by Experiment V-D. Therefore: (1) from the fact that the intermediate segment of the external geniculate body is the macular projectional segment (Rönne, Brouwer-Zeeman), (2) from observations that in pathological cases where the macular or the "central" vision is disturbed the pole of the occipital lobe was damaged (Henschen, Holmes *et al.*), (3) from the fact that the inter-

³ That in the human brain the fibers of the upper horizontal branch reach also directly the upper lip of the calcarine fissure is demonstrated by the case of Balado-Adrogue-Franke, and by my anatomical-pathological cases not yet published.

mediate perpendicular branch (forming in reality the "middle" or axial segment or "rib" of the external geniculo-cortical fiber "fan") has its own course and terminates in the pole of the occipital lobe (Experiments I, IV, and especially V-A), (4) further from the fact that the intermediate segment of the external geniculate body degenerates after the destruction of the macular portion of the striate area (Experiment V-D), and also considering other factors with which I will deal later,⁴ I feel entitled to conclude that the intermediate vertical branch of the visual radiation transmits impulses from the homonymous halves of both maculae upon the pole of the occipital lobe and, in the monkey, to its external face called the occipital operculum (figs. 22, 23; for arguments against the so-called bilateral cortical representation of the macula see this discussion later).

The lower horizontal branch of the external sagittal layer has not been injured in any of the present experiments. Nor, except for a few solitary fibers, has any degenerated bundle been seen to enter the lower lip of the fissura calcarina. This negative result valued in its proper significance in connection with the positive results in the present experiments appears really as a positive result. We would appear to be amply justified in accepting the termination of the lower horizontal branch of the external sagittal layer as being in the lower lip of the fissura calcarina and it is safe to regard these ventral bundles of the visual radiation as reaching the lower lip in a similar way, though in reversed fashion, as has already been described for the dorsal bundles. The ventral bundles bend gradually in a spiralsense in their course occipitalward below the posterior horn of the lateral ventricle, at the same time approaching medially the lower lip of the fissura calcarina. They have their separate course, as described, since the dorsal horizontal and the perpendicular branches, degenerated in the present experiments, do not mix with them; and no degenerated bundles from the dorsal or from the perpendicular branches have been seen to descend toward the lower lip. The only possible origin of the bundles which form the ventral portion or ventral "rib" of the fiber "fan" of the visual radiation is the external or lateral segment of the external geniculate body.⁵ This is well ascertained by our Experiment V-B.

⁴ Compare also Brouwer-Heuven-Biemond, Heuven, Brouwer, 1930; R. A. Pfeifer, 1930; Foerster, 1929, and Foerster-Penfield.

⁵ That the lateral segment stands in connection with the lower lip has been lately proved by experiments of Heuven.

Accordingly, it is the ventral horizontal branch of the visual radiation which transmits impulses from the inferior extramacular quadrants of the homonymous halves of both retinae upon the lower lip of the fissura calcarina (figs. 22, 23).

Furthermore, it has been noted in the present experiments that the most dorsal and at the same time the most anterior bundles of the visual radiation, after they complete the spiral turn inward, become the most medial and supply a narrow strip of the striate cortex stretching along the inner boundary of that cortex in the upper lip of the fissura calcarina. If the same arrangement in the lower lip is accepted, as it must be, it becomes evident that the most dorsal and the most ventral bundles of the entire visual radiation supply a narrow striate zone of the fissura calcarina which actually forms a crescent with one of its horns in the upper lip and the other in the lower lip. This crescent turns both its horns occipitalward and its middle convex portion oralward toward the splenium of the corpus callosum, descending here into the bottom of the fissura calcarina, where both horns of the crescent are linked together (fig. 23).

These most ventral and most dorsal bundles of the visual radiation must, accordingly, transmit impulses from the most "peripheral" portion of the retina to a narrow "boundary zone" of the striate cortex, lining both the lips and the anterior portion of the bottom of the fissura calcarina.

The question of the finer projection of the individual macular quadrants upon small portions of the intermediate segment of the external geniculate body has not as yet been completely solved. Considering, however, the evidence for very sharp localization in this segment of the mentioned nucleus, which has come from the work of Overbosch (see also Brouwer-Zeeman, 1926), and which is well illustrated by our Experiment V-c, it is more than plausible that we have a definite localization of macular quadrants in definite portions of the intermediate segment of the external geniculate body. It appears logical to suppose the location of the projection of the upper homonymous macular quadrants to be close to the internal segment of the external geniculate body (where upper "peripheral" quadrants are projected), and to suppose the location of the lower homonymous macular quadrants to be close to the external segment (where lower "peripheral" quadrants are projected). Since the perpendicular branch of the external sagittal layer belongs to the macular portion of the visual radiation, a similar arrangement must

exist here also. This was in fact found. Thus the upper half of the perpendicular branch of the external sagittal layer near the dorsal horizontal branch (vr_1 in Experiment I and also in Experiment IV) would correspond with the upper quadrants of both homonymous hemimaculae, the lower half (approximately vr_2 bundle in Experiment I) with the lower quadrants of both homonymous hemimaculae.

From the above statements the following sequence of the bundles constituting the visual radiation imagined in cross-section through a hemisphere (for example, figs. 13, 39, 55, 56, 69, 71 and compare with f in fig. 23) can be constructed, beginning with the most medial or internal bundles of the upper horizontal branch of the external sagittal layer, then following that branch lateralward and descending along the perpendicular branch to the lower horizontal branch, and coming back medialward to the most internal bundles of the ventral branch: (1) the most peripheral monocular portions of the upper quadrant of the crossed retina, (2) the more internal, binocular portions of the upper extramacular quadrants of both homonymous hemiretinae, (3) the upper quadrants of both homonymous hemimaculae, (4) the lower quadrants of both homonymous hemimaculae, (5) the more internal, binocular portions of the lower extramacular quadrants of both homonymous hemiretinae, and (6) the most peripheral, monocular portions of the lower quadrant of the crossed retina.

This fairly simple arrangement of the various bundles of the visual radiation, deduced from purely anatomical investigations means a perfect "vertical articulation." If tested as to its value for human pathology it harmonizes well with the differing clinical symptoms found in varying lesions of the visual apparatus as will be explained subsequently. It also substantiates the hypothesis of Rönne (1919) deduced from clinical observations. (Compare also Heuven, p. 52; compare also remarkably similar ideas expressed long ago by Ewens, p. 485, and to some extent by A. Meyer.)

3. PROJECTION OF THE RETINA UPON THE CEREBRAL CORTEX

As to the projection of various retinal quadrants in the cerebral cortex of the monkey, and similarly in man, the following can be deduced from the present experiments (figs. 22 and 23):

The upper quadrants of both homonymous hemiretinae, excluding the macula, are projected upon the upper lip of the fissura calcarina; the lower quadrants upon the lower lip. The horizontal meridian

dividing the upper quadrants from the lower, except the macula, corresponds with the bottom of the fissura calcarina (in cases with an equal stretch of the striate area in both lips). The most peripheral portion of the retina, the temporal crescent, is projected upon the most anterior portion of the floor and upon both lips of the calcarine fissure. Consequently the "peripheral" boundary of the nasal half of the retina corresponds with the boundary of the striate area, lining the fissura calcarina. The validity of the improbable assumption that in the human brain the temporal crescent is entirely accommodated by the lower lip must be determined by future investigations. (Compare Foerster, 1929; that the temporal crescent is represented also in the human brain in both lips of the calcarine fissure is supported by the case of Balado-Adrogué-Franke where fibers of the upper lip were interrupted with the resulting inferior crescentic hemianopsia [mainly]). The macula lutea is projected upon the most posterior portion of the fissura calcarina, principally upon the pole of the occipital lobe and, in the monkey, upon the occipital operculum. Between the temporal crescent and the macular cortex the binocular "peripheral" portion of the representation of the retinae is placed. The horizontal meridian dividing the upper quadrants of both hemimaculae from their lower quadrants corresponds approximately with a horizontal line, which can be imagined as a caudal continuation of the bottom of the calcarine fissure encircling the pole of the occipital lobe and stretching across the occipital operculum toward the fissura simialis. It divides the occipital operculum into an upper and a lower half of somewhat unequal size (approximately *Sos* in fig. 21). The vertical line dividing the left and right halves of both maculae corresponds in the monkey with the anterior limit of the striate area covering the occipital operculum and stretching approximately parallel to the sulcus simialis (*Ss* in fig. 21). Here, also, approximately at the midpoint of the oral boundary of the striate area have to be localized the points of fixation (*x* and *y* in fig. 23). Since the extramacular quadrants have in their cortical representation an approximate shape of a crescent which embraces the macular cortex in front and both dorsally and ventrally, the dorsal and ventral horns of this crescent can be imagined as ending in thin, sharp points. The dividing line between the left and right halves of the extramacular cortex would therefore be lost or obliterated.⁶

⁶ Compare the almost identical view concerning the projection of the retina upon the cerebral cortex in the monkey shared by Brouwer-Heuven-Biemond and by Heuven.

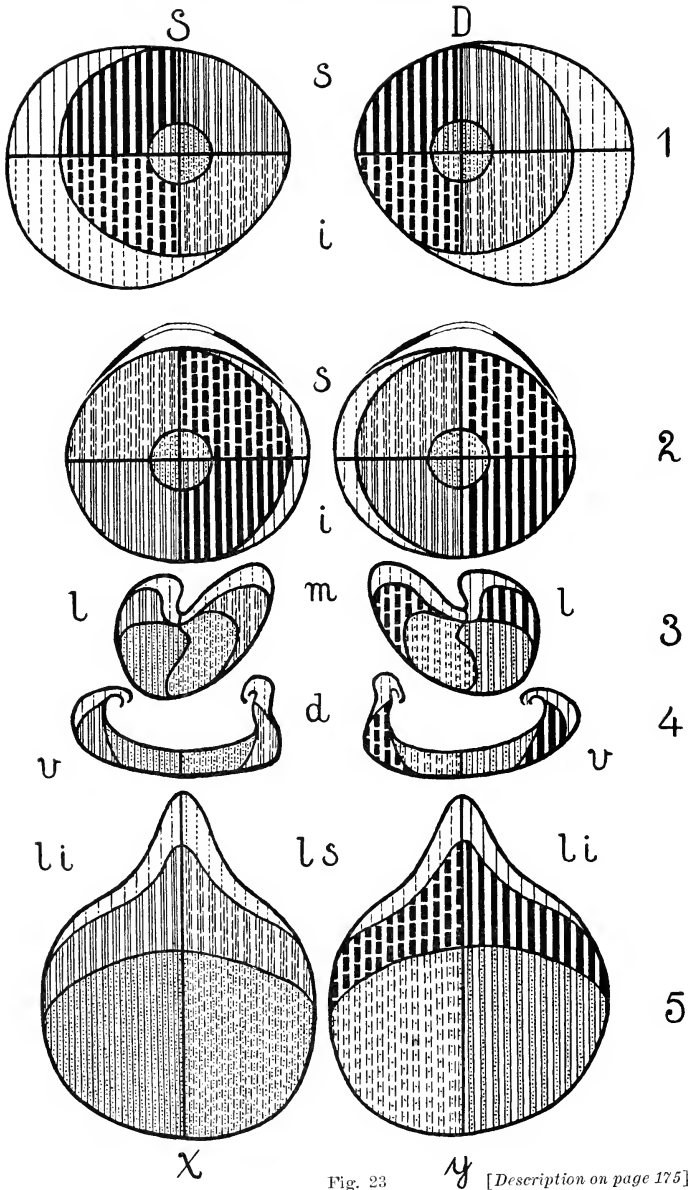


Fig. 23 [Description on page 175]

The projection of various retinal quadrants upon the occipital lobe expounded in the above lines stands in good accord with the distribution of excitable points for conjugate eye movements in the occipital lobe of the monkey found by Schäfer, Mott-Schäfer, Lewandowsky-Simons, Levinson, Bárányi-Vogt, and with the results of the electrical stimulation of various portions of the striate area in man undertaken by Foerster, 1929, and Foerster-Penfield.

The anatomical facts found here, physiological experiments (Munk) and clinical observations (Laqueur, Lenz, Henschen, Holmes, Foerster 1929, Souques-Odier, Brouwer, R. A. Pfeifer, *et al.*) all compel us to conclude that the macula, or better, both the homonymous hemimaculae, must be represented in the posterior portion of the striate area around the pole and occipital operculum and not in its anterior portion (fig. 23). The macular segment of the external geniculate body, as found by Rönne (1914) and by Brouwer-Zeeman (1926), represents a large portion of that nucleus, perhaps more than half of it. The fibers which originate in this segment, as we observed, constitute a considerable portion of the visual radiation, nearly half of it, namely the

Fig. 23. A diagram to illustrate the projection of various quadrants of the visual fields and of both retinae upon the external geniculate bodies, upon the visual radiation, and upon the visual projection area of the cerebral cortex (area striata), as determined by the present experiments, combined with those of Brouwer-Zeeman. Left (*S*) and right (*D*) sides of the visual fields and of the afferent visual apparatus. Number 1 represents both fields of vision with their upper (*s*) and lower (*i*), nasal and temporal halves; the smaller inner circles represent the "central" or macular portions (their relative size in comparison with the perimacular portion is somewhat exaggerated); the large circles represent the peri- or extramacular portions of the binocular visual fields; the outermost lightly shaded sickle-shaped zones represent the monocular portions of the visual fields. Number 2 represents left and right retinae with their upper (*s*) and lower (*i*), nasal and temporal halves; smaller and larger circles and the monocular portions as above. Number 3 represents a schematic cross section through the left and right geniculate bodies; their internal margins (*m*) close to the thalamus; their external margins (*l*); their concave contours in the figure facing upward represent their ventral margins. Number 4 represents cross sections through the left and right visual radiation (external sagittal strata of the parieto-occipital lobes); their dorsal horizontal branches (*d*), their ventral horizontal branches (*v*) with perpendicular or vertical branches (in the figure horizontal) connecting both horizontal branches. Number 5 represents the left and right visual projection cortex, the area striata of Elliot Smith, field 17 of Brodmann, each subdivided into an upper (*ls*) and a lower half (*li*) corresponding with the upper and lower lips of the calcarine fissures. The dividing lines, vertical in the figure, and terminating at the letters *x* and *y*, correspond in their upper parts to the bottom of the calcarine fissures and to the horizontal meridians of both visual fields dividing the upper from the lower extramacular quadrants; in their lower parts (lower in the figure) these lines correspond to horizontal meridians dividing the upper from lower macular quadrants. The points where these lines reach the posterior limits of both striate areas, marked by the letters *x* and *y* in the figure, correspond to both points of fixation in the visual fields. The vertical lines or meridians dividing the left from the right homonymous halves of the macular portion of the visual fields correspond to the posterior (lower in the figure) circumference of the striate areas close to the letters *x* and *y*.

perpendicular branch, a fact quite in accord with the greater importance of "central" or macular vision and with the greater number of ganglion cells of the fovea centralis (compare Woollard). Macular fibers form the perpendicular branch interposed between both horizontal branches. They enter neither the upper lip, nor the lower lip of the fissura calcarina but the pole and the operculum of the occipital lobe (figs. 13, 22, 23). It is also true that the visual fibers which enter the occipital pole and the operculum are of a more delicate caliber than those terminating in the lips of the fissura calcarina (its anterior portion). This harmonizes well with the delicate discriminating function of the macula and the more summary, reflex function of the "peripheral portion of the retina."

Besides this direct proof, still another consideration leads us to the same conclusion. Since the number of macular fibers in the optic nerve and tract exceeds that of the extramacular fibers and since the macular segment of the external geniculate body represents more than half of that nucleus, the macular cortex must be proportionally large, probably larger than the entire extramacular cortex. It is logical, therefore, to search for the macular cortex in the far more extensive region of the striate area which covers the occipital pole and, in the monkey, the occipital operculum, than in the narrow strip of the striate cortex lining the fissura calcarina. In the monkey's brain, the striate cortex which remains hidden in the fissura calcarina represents only about a half of the whole striate area (field 17 in fig. 7, compare with figs. 4, 21, 24). Evidently there is not enough room for the extensive macular projection in the fissura calcarina, certainly not in the brain of the monkey. (Compare also Brodmann, 1909, p. 218.)

In the human brain the conditions are somewhat different from those in the monkey, though not essentially. Less of the human striate area extends over the occipital pole and still less over the convex face of the occipital lobe (according to Brodmann in 10 per cent of cases; see also Goldstern and Economo). The greater portion of the human striate area remains hidden in the fissura calcarina and extends but slightly into the immediate neighborhood. There is, therefore, in the human brain proportionately less of the macular cortex on the convex face of the occipital pole than in the monkey, a part of the human macular cortex being buried in the most posterior portion of the fissura calcarina. But in both man and the monkey the anterior portion of the fissura calcarina represents the extramacular portion of the retinae. (Compare also Heuven, p. 60.)

It is also noteworthy that both in the human and the monkey brain the calcarine fissure usually remains in its anterior portion (that closer to the corpus callosum), a simple undivided furrow. The change in this respect occurs fairly suddenly near the occipital pole where regularly, in the monkey brain, the *fissura calcarina* divides into two branches, an ascending and a descending branch. (Compare figures in this treatise showing the inner face of the hemisphere.) This can be explained only in the sense of a rapid increase in the size of the striate area in its posterior portion. It is the posterior portion of the striate area which in the phylogenetic scale, with the perfection of "central" or macular vision and with the more perfect structural development of the macula lutea, undergoes the greatest expansion, while the oral portion of the striate area participates in these changes only moderately.

Clinical experiences with small scotomata affecting "central" or macular vision can only be understood by accepting a thin and yet a broad macular segment of the visual radiation, which the vertical branch of the radiation actually is, and an extensive cortical representation of the macula. (The necessity of accepting a wide macular projection area was recognized by most investigators studying the visual apparatus, though this led to the erroneous acceptance of a multilocular or a "diffuse" projection upon an extensive region of the cerebral cortex; see for example Monakow.) If the macular fibers were collected into a tiny, compact fascicle as imagined by some investigators, and the macular cortex were a small region in any way comparable proportionally to the small size of the macula lutea as compared with the remaining portion of the retina, macular vision would be usually completely abolished even by subcortical or cortical lesions of a moderate extent. Since, as we saw, the perpendicular macular branch represents a considerable portion of the entire visual radiation and the macular cortex also is a wide region, only extensive injuries will result in complete annihilation of macular vision. Small subcortical lesions, on the contrary, because of the peculiar distribution of macular fibers in a fairly thin though broad lamina, will be able to interrupt only a small segment of that lamina; and in the same way small cortical injuries will destroy only a small portion of the macular cortex, in both cases producing only small sharply delimited "central" scotomata. Multiple lesions of the macular vertical branch interrupting a great number of individual fibers and finest fascicles will result in no circumscribed loss of the visual fields determinable by present

methods but in a decrease of the acuity of the "central" vision (as for example in disseminate sclerosis; compare Herrman, 1929).

In the occipital operculum of the monkey's brain there can regularly be observed a shallow sulcus or impression running somewhat obliquely horizontal across the occipital lobe from the occipital pole toward the sulcus simialis (*Ss*), terminating not far from the latter in a shallow notch and dividing the operculum into an upper and a lower half (*Sos* in fig. 21, sulcus occipitalis superior of G. Elliot Smith, sulcus calcarinus externus of Cunningham-Smith, in anthropoids and in man). This sulcus might well correspond, in my opinion, to the horizontal meridian dividing the upper quadrants of both homonymous hemimaculae from the lower quadrants. Its cortex receives particularly dense bundles of the fine afferent visual fibers. It would seem, then, that this shallow impression corresponds to the spot of the most discriminative and the most analytic vision, that is, to the fovea centralis of the retina. This sulcus, especially its anterior notch, would in fact be a fovea (recte hemifova) centralis corticalis.

Objections have been made in recent times to the conception of a fixed anatomical point to point projection of the retina upon the visual cortex, especially of the macula (Goldstein, Fuchs). It has been claimed that in cases of a central destruction of the macular cortex the formation of a new "functional macula" was observed. The position of this functional macula, accordingly, would correspond with an eccentric spot of the hitherto extramacular portion of the hemiretinae. But from the anatomical point of view it is inconceivable how the highest organized and most perfectly differentiated structures of the visual system, as undoubtedly the macular portion is (compare Cajal), could in the adult and in a short time be substituted in such a perfect way by the obviously less perfectly organized extramacular retina and the corresponding portion of the visual system. It can be granted that such a new "functional macula" could perhaps become the "central spot of the still functioning portion of the retina" and of the rest of the visual fields; yet the function of such a "pseudomacula" would necessarily remain less perfect than that of the normal macula.

To explain certain clinical symptoms observed in many, though not in all cases of the hemianopsia of central origin, some investigators thought it convenient to recur to the hypothesis of a double or a bilateral representation of the macula (Heine, Jendrassik, Lenz, Wilbrand, Henschen, R. A. Pfeifer, Niessl von Mayendorf, Foerster,

1929, *et al.*). Each macula, according to this hypothesis, would be projected upon both hemispheres in such a way as to bring each small segment of each total macula or even each of the macular cones in connection with the visual cortex of both hemispheres. Thus, if one of the visual cortical centres or its afferent fibers were destroyed, nevertheless, both total maculae would still remain in connection with the hemisphere remaining undamaged. This hypothesis would explain why macular vision is so often preserved.⁷ But, briefly, this would not explain why in other cases of hemianopsia there is no sparing of macular vision, nor, why a unilateral partial destruction of the visual cortex or of its radiation produces absolute, permanent, and very sharply delimited central scotomata (compare, for example Holmes, 1919; Wilbrand, 1926). That the hypothetical decussating macular fibers from the ipsilateral homonymous hemimaculae (with respect to the seat of the lesion in the occipital lobe) cannot use the optic chiasm to reach the opposite hemisphere is proved by the fact that macular vision is not spared in cases where the optic tract is completely interrupted. In such cases macular vision shows the affection of a hemianoptic character most frequently with the vertical line passing exactly through the points of fixation. A partial crossing of the macular portion of the visual radiation through the corpus callosum was, therefore, supposed. Some investigators even claimed to have seen the decussating bundle of the macular fibers, a "fasciculus corporis callosi cruciatus," converging toward the corpus callosum (Niessl von Mayendorf, R. A. Pfeifer). Thus, if the lesion interrupting the visual radiation were situated far enough from the point of decussation or if the visual cortex on one side were injured, the impulses from both total maculae would, nevertheless, reach the undamaged hemisphere by way of the corpus callosum. But this hypothesis is also weak since it does not give a satisfactory explanation for the "central" scotomata of cortical origin.

As has been said in the foregoing paragraphs, no decussating fibers of the visual radiation were seen in any of the present experi-

⁷ The supposition, that in all cases of hemianopsia where there is no sparing of the macular vision macular cortical regions in both occipital lobes have been damaged (Lenz), is too artificial to be probable (although in rare cases such a bilateral damage may occur). Also that would not explain why in such hemianopsias the macular vision is preserved on the functioning sides in spite of the bilateral damage to the macular cortex. Finally, the explanation of the preserved macular vision, usually found in cases of hemianopsia, in the sense of the preserved "remnant" of the visual fields ("Gesichtsfeldrest") is no explanation at all.

ments.⁸ This radiation above the external geniculate body and as far as the cerebral cortex is strictly unilateral. Accordingly, a bilateral cortical representation of each total macula cannot be accepted, as justly pointed out by Harris, Holmes-Lister, Igersheimer, Holmes, Souques-Odier, Brouwer, Uhthoff, Best, Kleist, *et al.* The sparing of the macular vision in many cases of hemianopsia cannot, therefore, be explained by the hypothesis of a bilateral cortical representation of the total maculae. Its cause must lie in the peculiar position of the macular portion of the visual radiation and the macular cortex.

On several occasions it has been emphasized that the macular portion of the visual radiation cannot be a tiny, compact fiber "bundle." The macular fibers in fact represent a considerable portion of the radiation, namely its perpendicular branch. On the other hand, the macular cortex, being situated in the occipital pole, and in the monkey in the occipital operculum, occupies a position separating it from the remaining striate cortex which represents the extramacular retina. The position of the macular cortex in fact rather exposes it to various injuries, and undoubtedly this is the case in some respects. Yet in the human brain it is exactly that portion of the visual cortex which is partly hidden in the deep posterior portion of the fissura calcarina where the latter usually splits into two branches. It also ought to be considered that the extramacular striate cortex occupying both lips of the fissura calcarina, these latter adjoining each other, together with both horizontal branches of the visual radiation, forms a topographical and patho-physiological unit which can be injured independently of the macular cortex (for example case Nordenson, see Henschen, 1919 or R. A. Pfeifer, 1930). Another important feature is the separation of the calcarine fissure, a frequent seat of pathological processes (see Best), from the perpendicular macular branch of the external sagittal layer by the posterior horn of the lateral ventricle, by the tapetum, and by the internal sagittal layer. It is obvious that if a pathological process destroys the anterior portion of the calcarine fissure, but leaves the occipital pole undamaged, and does not penetrate through the ventricle or exert a pressure upon the macular radiation beneath,

⁸ Neither Wenderowicz, Putnam, nor Fleehsig (1927) were able to ascertain the existence of such fibers. It is also important to mention that Brouwer and his collaborators in the recent experiments with monkeys in which the striate area of one side was destroyed, were unable to discover any changes in the cells of the contralateral external geniculate body, which would certainly be found if a part of the visual radiation decussates. (According to a personal communication from Professor Brouwer; see also Brouwer-Heuven-Biemond and Heuven, p. 52.) With this our Experiment V-D and V-E stands in a perfect accord.

both macular fibers and macular cortex will escape injury. In such a case the entire extramacular portion of the homonymous halves of the visual fields including the temporal crescent can be eliminated, producing a "peripheral" or incomplete homonymous hemianopsia with macular vision preserved. In this case, the "central" vision of the hemianoptic side will remain in every respect perfectly preserved since the association connections between the striate cortex covering the occipital pole, and the area peri-parastriata will not be damaged (see figs. 25, 86-94 of Experiment XIV). In the case of a tumor, however, originating from the internal surface of the hemisphere close to the splenium of the corpus callosum, it is likely that the initial hemianopsia with intact "central" vision will in the course of the illness develop into a complete hemianopsia when the pressure is sufficient to interrupt the deeply situated macular fibers. The appearance of hemianoptic symptoms with macular vision intact can, therefore, be expected most frequently in those pathological processes involving the cortex of the fissura calcarina, where the pressure is slight or entirely absent (encephalomalacic and thrombotic processes, see Best). With both lips of the calcarine fissure lying close together and with both horizontal branches of the radiation being closer to the inner face of the hemisphere, if the destruction is extensive enough, both upper and lower homonymous quadrants of the visual fields will be affected without the impairment of the central vision.⁹ But, as it is easy to understand, this must not necessarily occur if only one of the lips of the fissure is destroyed. Here, too, "central" vision will remain unimpaired in case if neither the retro-calcarina nor the perpendicular branch of the visual radiation (which is fairly distant from the lateral cortex) are affected by the pathological process; but the upper or the lower macular quadrants will be included in the blind portions of the visual fields if the lower or upper halves of the macular cortex or if the lower or upper half of the vertical branch have also been damaged. It can also be understood, and such cases have been reported, that a pathological process can destroy both lips of the fissure and in addition the cortex on the convex face of the occipital lobe (areas 18 and 19 of Brodmann), and

⁹ Since both lips of the calcarine fissure are supplied by one single artery (*arteria fissurae calcarinae*), any damage to it or any pressure upon it will usually impair both lips in a symmetric way. This makes it possible to understand why most of the preserved macular portions of the visual fields exhibit regular boundaries and have in various cases a different size depending on the extent of the injury.

yet macular vision will be unaffected if the posterior portion of the striate area and the macular portion of the visual radiation remain normal. (Such a combination of destruction can also occur bilaterally, in both hemispheres, leaving macular cortex and macular radiation intact). Here, however, there is likely to be some impairment of vision, especially of the higher cognitive processes, even if the macular cortex is not directly affected, since its association and other connections will be interrupted. If the pathological process penetrates deep enough either from the internal or external face of the hemisphere and attains the vertical branch, or if it extends over the posterior portion of the striate area (occipital pole), the initial incomplete hemianopsia will become complete, the macular vision preserved at the beginning will finally be destroyed. In such a case the vertical dividing line between the blind and normal halves of the visual fields will pass exactly through the points of fixation.¹⁰

It is clear from the foregoing that the hypothesis of a bilateral cortical representation of the macula besides being hardly consistent with a point to point macular projection proved by the existence of small, sharp macular scotomata, is neither anatomically justified, nor necessary to explain the preservation of macular vision observed in many cases of hemianopsia. The projection of the maculae upon the cerebral cortex must be imagined as similar to that of the extramacular binocular portions of the retinae. The macula is divided by a vertical meridian into two halves, each of these being projected upon another hemisphere. This is accomplished in such a way as to bring homonymous halves of both maculae in connection with one hemisphere only. Accordingly, when the visual cortex of one hemisphere, or only the macular cortex or its afferent fibers are completely destroyed, the result will be a complete and lasting homonymous macular hemianopsia with the vertical line passing exactly through the points of fixation and dividing hemianoptic halves of both macular visual fields from the opposite halves remaining in function. Nor do the theoretical arguments brought forward in support of the hypothesis of a double cortical representation of the total macula seem to be

¹⁰ The peculiar arrangement of the various segments of the visual radiation, as found in the present study, explains also the often observed complete hemianopsia in cases where the lesion lies close to the geniculate body. Here all the fibers, both macular and "peripheral," lie closely assembled and are likely to be interrupted by a single lesion, while more posteriorly the macular fibers take a protected position on the outer side of the lateral ventricle. This is an additional argument which renders the supposition of the decussating macular fibers superfluous.

valid. If every macular cone were in connection with each striate area, according to the principle of identical cortical representation of homonymous points, this would, it seems, annihilate any stereoscopic effect of binocular vision. Also, the individual differences in the size and shape of the macular portion of the visual fields preserved in cases of hemianopsia can easily be explained without resorting to an additional hypothesis of a varying degree of double macular representation in various persons, since it is natural that the destroyed portion of the perimacular cortex or of the perimacular portion of the radiation will vary according to the individual case.¹¹

Our conclusion is: no evidence and no necessity exist for accepting a bilateral cortical representation of each total macula in the sense of Wilbrand, Lenz, *et al.*¹² The preservation of macular vision must be explained by the (1) separate course and protected position of the macular portion of the visual radiation and a well protected location of the human macular cortex, and (2) by the close position of those portions of the striate area which represent extramacular portions of the visual fields, in both lips and in the bottom of the fissura calcarina, which arrangement renders separate injury to these latter regions possible (besides the multiple blood supply of the pole of the occipital lobe).

4. FUNCTION AND DISTURBANCES OF THE VISUAL RADIATION AND OF THE VISUAL PROJECTION CORTEX

Since projection of various quadrants of the hemiretinae upon definite portions of the visual cortex and the arrangement of definite bundles of the visual radiation are as described at the beginning of this chapter, it is easy to understand that various symptoms follow variously situated cortical or subcortical injuries to the visual system.

¹¹ Further, not only does the hypothesis of a bilateral representation of each total macula inadequately explain the escape of macular vision in cases of ordinary vertical homonymous hemianopsia, but it explains the macular escape when the superior or the inferior quadrants are abolished bilaterally less well. In fact, to apply the principle of a bilateral macular representation as an explanation of superior or inferior incomplete hemianopsia it would be necessary to construe an additional hypothesis: that of a projection of each total macula upon the upper and as well upon the lower half of each macular cortex.

¹² Foerster's (1929) case in which after unilateral removal of the occipital lobe and section of the splenium of the corpus callosum, a complete hemianopsia without sparing of macular vision followed, can hardly be ascribed to the interruption of hypothetical decussating macular fibers. A contrary conclusion would be unavoidable had the corpus callosum not been damaged and had the macular vision remained unimpaired (providing that one occipital lobe had been completely removed).

Since there exists a stable, or fixed arrangement of functionally different bundles of the visual radiation, symmetrical in both hemispheres, and a similar distribution of cortical representations of retinal quadrants, the symptoms produced by various pathological processes or by injuries will largely depend on the size, location, and direction of the injuries.

Unilateral injuries or pathological processes which are limited to the occipito-parietal and temporal lobes, will produce:

(1) a complete homonymous hemianopsia of the opposite side with the vertical dividing line passing exactly through the points of fixation if one entire striate area is destroyed (since the striate area represents an extensive curved surface not lying in one plane this explains why portions of the visual fields so often remain unharmed, especially in gunshot injuries producing a channel more or less straight);

(2) an incomplete homonymous hemianopsia of the opposite side with macular vision preserved if one entire striate area lining the *fissura calcarina*, except its posterior portion and the occipital pole, is destroyed. The latter can be produced not only by tumors, malacic processes, bleedings, etc., but also by injuries if they are followed by subsequent haemorrhage with destruction of both lips of the *fissura calcarina* and leave the macular fibers of the visual radiation and the pole of the occipital lobe undamaged. On the other hand, it is easy to understand why gunshot injuries will rarely produce such a form of hemianopsia without infringing in some way or another on a portion of the macular fibers or of the macular cortex. If the position of the gunshot channel is in the horizontal plane, but perpendicular to the long axis of the hemisphere, this will produce either an inferior quadrant hemianopsia with the preservation of the macula if the upper horizontal branch of the external sagittal layer alone is destroyed, or a rarer superior quadrant hemianopsia if the inferior horizontal branch alone is interrupted. But it is likely that either the dorsal or the ventral half of the vertical macular branch of the visual radiation will also be damaged, thus completing the hemianoptic loss up to the points of fixation, in the upper or in the lower visual quadrants, depending on whether the lower or the upper half of the perpendicular branch of the radiation is interrupted. If the gunshot channel runs in longitudinal direction but near the median line, it will destroy both lips of the *fissura calcarina*, while not necessarily destroying the macular fibers. More likely than not the macular

cortex will also be damaged in such a case. Yet it is improbable that the macular cortex will be destroyed on one side and be unimpaired on the other. The result will almost surely be an incomplete or complete hemianopsia of the opposite side with perhaps hemianoptic scotomata of the same side;

(3) if only the occipital pole is destroyed this will produce a "central" homonymous hemianopsia of the opposite side. A partial injury of the occipital pole will produce, if the lower half of the occipital pole is destroyed, superior quadrantic macular hemianopsia; if the upper half is destroyed, an inferior quadrantic macular hemianopsia. Small injuries to the macular cortex will produce small congruent homonymous scotomata of the corresponding macular quadrants, usually of an irregular shape;

(4) partial destructions of the striate cortex in the anterior portion of the fissura calcarina will result in congruent homonymous scotomata of various forms in the perimacular or the "peripheral" portions of visual fields, except when the most oral or also the most "peripheral" zones of the striate cortex along the upper and the lower lip are destroyed; in which case portions of the temporal crescent will be added;

(5) if the fringes of both lips of one fissura calcarina and the bottom of that fissure in its anterior portion are damaged (for example by superficial cortico-malacic and similar processes) there will be an isolated loss of the opposite "temporal crescent." If the bottom of that fissure, besides the fringes of both lips, is also involved in the destruction, including portions closer to the occipital pole, a temporal crescent-hemianopsia will be accompanied by an ordinary hemianopsia of the extramacular quadrants of both visual fields. It is also easy to understand why loss of vision in the temporal crescent alone is a rare symptom. It is seldom that the anterior portion of the fissura calcarina and its fringes suffer an isolated destruction without impairment of either the visual radiation (at least both horizontal branches), or other more "centrally" located portions of the striate cortex nearer the occipital pole. On the other hand the nearness to the falx cerebri of the anterior portion of the striate area and of the bundles of the visual radiation supplying it (both most dorso-antero-medial and ventro-antero-medial bundles of the horizontal branches first entering into the fissure) can explain the impairment of the temporal crescent as an initial symptom of pathological processes near the splenium of the corpus callosum or even of tumors in distant

regions of the hemisphere, e.g., of the frontal lobe, since that part of the visual radiation will be pressed against or pulled onto the posterior margin of the falx and to the tentorium.¹³ (There is no need therefore of supposing a "wide" representation of the visual function in the hemisphere.) Later on, when the pressure or pathological process extends into the more caudally situated portions of the striate area and to the visual radiation beneath, incomplete or a complete homonymous hemianopsia will develop;

(6) the peculiar arrangement of the upper and lower "peripheral" segments of the visual radiation, appearing on cross sections through the hemisphere as the upper and lower horizontal branches of the external sagittal layer, with the macular perpendicular branch between them, renders possible a fairly isolated injury of either of the above mentioned branches, followed by loss of the particular extramacular or macular quadrants or of the entire homonymous halves of the fields of vision. Yet the same position of the visual bundles will not readily allow the interruption of both upper and lower horizontal branches of the radiation by a single traumatic injury. For instance, there could hardly occur gunshot injury damaging both of the horizontal branches without some injury to the macular branch. The only possible course of such an injury which would abolish both extramacular quadrants of the visual fields and yet spare macular vision would be a gun shot channel perpendicular to the horizontal plane of the hemisphere and a little away from the falx cerebri yet medially from the plane of the perpendicular branch. (That this would hardly be consistent with the preservation of life is not necessary to point out.) The macular vision will be affected if a gunshot channel has a fairly exact horizontal direction from outside inward, more or less perpendicular to the long axis of the hemisphere, interrupting the perpendicular branch. Since it would probably injure the fissura calcarina itself in its more oral portion there would at the same time be an impairment of the extramacular portions of the visual fields in the form of "peripheral," perhaps multiple scotomata of various forms with a portion of the extra-macular visual fields spared. Such a complicated impairment of the visual fields proved indeed puzzling

¹³ Such or a similar mechanism might account for the crescentic hemianopsia in some cases reported by Allen (1930), where the seat of the tumor was on the external face of the occipito-parietal lobes. Compression of both the upper and lower horizontal branches of the visual radiation against the falx cerebri and tentorium, and squeezing of both lips of the calcarine fissure (anterior portion), while the perpendicular branch situated deep in the hemisphere escapes at first from the effect of such a pressure, could cause such an hemianopsia.

for the "decentralistic" attempts at explanation (see Monakow, 1914, pp. 406, 407).

Lastly, without going into further details of possible combinations of injuries of the central visual apparatus and the various symptoms produced in these ways, it should be mentioned that unilateral symptoms can be combined with bilateral symptoms if the opposite hemisphere is at the same time injured. Since the position of the visual radiation and of the striate areas in the two hemispheres is symmetrical, the injuries, e.g., gunshots which course horizontally and with their direction more or less perpendicular to the long axis of the hemispheres or, what is almost the same thing, to the longitudinal axis of the visual radiation, will produce symptoms, on the whole, of a symmetrical character. If on the contrary, the direction of the injury varies from the horizontal plane, different portions of the visual mechanisms will inevitably be damaged on each side and asymmetric symptoms be produced. An almost symmetrical damage to the upper horizontal branches of the visual radiation on both sides owing to a malacic softening can also occur with the resulting incomplete inferior bilateral quadrant hemianopsia (blindness of the lower halves of both visual fields with the escaping of the macular vision), as one of my unpublished cases demonstrates.

From what has been said in the preceding pages on the projection of various extramacular and macular quadrants upon certain segments of the striate area, it can easily be understood that the cortical projection of the retina is not in every respect a faithful copy or replica of the retina. Although, in the main, the relative positions of small cortical segments remain the same as in the retina, the positions of quadrants appear, however, slightly or even considerably displaced with respect to each other. Their shape also is considerably changed. What appears preserved from the original "spatial" relations of the retina is preponderantly the relative or the mutual relation of small structural units, fiber bundles, and cell groups. The units which were contiguous in the retina remain neighboring in the central visual path and in the visual cortex. Thus, for instance, the macular fibers of the visual radiation, although almost entirely separated from the remaining fibers conducting impulses from the extramacular portions of the retinae, preserve among themselves their original mutual relationships. Only on two points does the macular perpendicular branch of the external sagittal layer touch the extramacular portions, viz., where it is continuous with the upper and lower horizontal branches. The

small areas of the visual cortex supplied by individual bundles of the visual radiation also have, as we observed, a different shape according to the region. Whereas the dorsal bundles (and also, as we must assume, the ventral) supply long narrow triangular strips of the fissura calcarina, the macular bundles supply cortical segments of a more condensed triangular form. There is good reason to suppose that all macular bundles supply such small triangles, with each of these triangles pointing its sharp wedge toward a central point corresponding with the points of fixation. (As we explained previously, the latter points have to be localized at the postero-lateral, or in the monkey at the lateral anterior limit of the striate area covering the occipital operculum.) Thus when a single macular bundle or segment of fibers is interrupted, small congruent homonymous triangular scotomata will result pointing their sharp wedges toward the points of fixation. This seems to be the only plausible explanation of the triangular shape of "central" scotomata which is usually found. But this also means that this form of scotomata hardly, if ever, will result in consequence of an injury to the macular cortex, but will result usually from a well delimited partial interruption of the macular portion of the visual radiation, since a purely cortical injury will hardly ever have the shape of a triangle corresponding exactly with the triangles supplied by individual bundles.¹⁴ If the extramacular cortex surrounded in circular or half circular fashion the entire macular cortex, similar to the retinal conditions, the appearance of a circular (recte semicircular) scotoma, the so-called "ring scotoma," or of a circular reduction of homonymous fields of vision, would be difficult to explain by single rectilinear cortical injury or by other similar pathological processes. But since the "peripheral" or extramacular cortex is situated mainly in the anterior portion of the fissura calcarina, that region can be easily damaged by a single and comparatively small injury. So also the pole of the occipital lobe can be destroyed separately producing "central" homonymous hemianopsia, or "central" scotomata.

¹⁴ This arrangement would also explain triangular "rests" of the visual fields in cases where the visual radiation is interrupted with the exception, however, of one single bundle (for example Uthoff, 1915, case 5; consult Lenz, 1924, fig. 15).

5. ORGANIZATION AND FUNCTION OF THE VISUAL SYSTEM
IN GENERAL

From the present investigations some further conclusions must be drawn, conclusions which bear on the general principle according to which the entire central visual apparatus is organized. In none of the five experiments (Experiments I, II, III, IV, and V-A) was the entire visual radiation caused to degenerate. By the experimental lesions made, a variable portion of the radiation was interrupted. In accordance with this in each of the five experiments not the entire visual cortex, but a part only, was found to receive degenerated fibers. The remaining visual cortex was found to be entirely free. Moreover, the visual cortex was found to be equally well supplied with afferent fibers. This fact favors the conception that each given small segment of the striate area is supplied by its own independent small bundle, and only by it. (This is supported also by Experiment V-B and V-c.) There does not exist, accordingly, a "diffuse" spreading of individual bundles of the visual radiation over a large segment of the visual cortex or even over the whole area striata. A "wide" cortical representation of the macula also does not exist. The size of the delimited cortical segments, different in each experiment, is in fair proportion with the size of the degenerated fiber segments. Where a single small fiber segment was interrupted, the supplied cortical segment is small. When two fiber segments were interrupted and in addition other fibers in neighboring segments degenerated, the cortex affected had a larger extent. Besides, two degenerated bundles were followed separately during their course up to the cortex; they become only seemingly mixed where they change their course, terminating, however, in different segments of the visual cortex. If the same segment was interrupted in different experiments, the supplied cortical segment proved to be the same. When the seat of the injury was slightly changed, a somewhat differently shaped cortical segment, although similar, was found to be supplied. Attention must also be called to the regular limits of supplied cortical segments (Experiments II, III, IV, and V-A). Most often these limits approach a straight line, though this has been denied. Such straight limits are due to the sharpness of the lesion in the external sagittal stratum of the parieto-occipital lobe, produced by a sharp instrument. Yet undoubtedly a sharp lesion would not suffice to produce such sharp limits if there did not exist a strictly regular, parallel arrangement of fibers of the visual

radiation. That such an arrangement indeed exists is further proved by one's ability to trace separate, individual bundles along their entire course corticalward. (Compare also Putnam.) The course of individual bundles of the radiation is, however, only approximately parallel. In places they diverge somewhat or approach one another since the visual fiber lamina adapts itself to the available space inside the hemisphere. Yet, on the whole, that entire lamina is composed of parallel bundles, which only gradually leave it to enter their respective cortical segments.

In addition to this in Experiment V-c, as also in other similar experiments not further reported here, where small lesions of various sizes and locations were made either in the visual cortex alone or also in the visual radiation, various parts of the external geniculate body degenerated. The size, location, and shape of the degenerated zones were in a fair proportion and agreement with that of the lesions. This means, of course, a point-to-point projection of the external geniculate body (and hence of the retina) upon the striate area.

The facts to which the present investigations have led, do not leave room for doubt as to the fundamental principle of the organization of the whole afferent visual system. Certainly no anatomical evidence exists for an "irregular" or a "diffuse" arrangement of bundles composing the central portion of the visual path. The evidence secured decidedly favors the "principle of localization," that is, of the projection of definite segments of the external geniculate body (and thus of the retinae) upon definite segments of the striate area. This is observed with all the rigidity of the logic postulated by the exquisite "spatial" function of the visual system and by the laws of physical optics. (Compare Chapter XIX.) Since this principle was found to be valid for the peripheral portion of the visual system, from the retina to the external geniculate body (Rönne, Brouwer-Zeeman, Overbosch), this means that the whole visual system is "spatially" organized. The collected evidence also refutes the supposition of an arrangement differing for the macular and extramacular portions. This also disproves the assertion that no finer, detailed projection of the retina upon the cerebral cortex exists, and that no such detailed projection can be proved. Another question, however, is whether the exactness and sharpness of the projection of the extramacular retina is the same as that of the macular portion. No doubt, however, can exist as to the actual projection of the extramacular or "peripheral" portions of the retina. In the macular portion of the

visual system, a very sharp projection must be accepted, segment for segment, point for point.

The visual projection cortex, according to my views, represents a fine mosaic of elementary units. These units are probably smaller in the portion representing the macula, than in those representing extramacular portions of the retinae. The individual elementary units of the visual projection cortex are each related to a definite "brush" of fibers since it must be accepted that the smallest conducting unit of the central link of the afferent visual path does not consist of one single neuron, but of a fascicle of several isodynamic neurons. We may look upon each such fiber bunch together with its correlated cortical cell group as representing in some sense an independent structural and functional unit or "element," a kind of a primitive visual system. Such a unit would be comparable to an elementary unit of the composite visual system of insects. A certain small peripheral stimulus, for instance, a light ray from a star falling upon a single retinal receptor, upon a cone of the fovea centralis, will be transmitted to the visual projection cortex by means of one single unit of conductors in the sense as defined above. In such a case only a single chain of neurons—that connected with the stimulated peripheral receptor—will be involved in the physiological process without substantial dynamic alteration of the next neighboring elementary units. An isolated reception, conduction, and transmission of the smallest discernible visual stimulus to the cortex by the above units appears as the structural mechanism and the functional principle underlying all visual "spatial" discrimination on which ultimately depends the complex process of vision in animals with a highly perfected visual apparatus. The "localizing signs" in the process of vision would, accordingly, be primarily due to the isolated arrangement of the above mentioned elementary visual units. The totality of these elementary units would give an appropriate mechanism for the perception, conduction, etc., of a multitude of light stimuli coming simultaneously to the peripheral receptor surface, the retina, that is, for a spatially continuous seizing and grasping of "pictures" or "figures" of larger external objects, and, with the lapse of time, for the change of shape, position and so forth (visual appreciation of space and time). According to this point of view the unity of a sum total of elementary visual stimuli derived from a larger object, or what is the same thing, the unity of the numerous stimulations of individual elementary structural visual units, would be achieved only after stimuli have reached

the visual cortex since, because of the isolation of the visual receptors and conductors, the integration of elementary excitations into "one whole" must be an exclusive cortical process.¹⁵ This would mean that the integration of a great number of independent visual stimulations, as far as "psychic" utilization is concerned, is not performed by any sub-cortical structures (at least in primates and in man). The regular "spatial" arrangement of elementary visual units: of peripheral receptors, of fibers of the optic nerve and tract, of nerve cells in the external geniculate body, of fibers of the visual radiation, and of the nerve cells of the visual projection cortex into sets of fiber bundles and into regular cell layers, is an indispensable mechanism for the "spatial" reception, "spatial" conduction, and "spatial" transmission of any kind of combinations of elementary light stimuli. Yet these can be brought together and fused into a single "total" impression only after entering the cerebral cortex. The regular arrangement of structural elements, of cells, and of fibers composing the afferent visual system, the equable distribution of afferent visual fibers to the entire visual cortex without any visible gaps or intervals in the supply, in a word, the arrangement of structural elements into "surfaces," into "laminae," and into "cables," and on the other hand the isolation of the elementary conductor units, the preservation of the "neighboring relations" of these units along their entire course up to the visual cortex, renders possible and guarantees the perception of "spatial" or "localizing" signs of light stimuli whatever their combination might be at a certain moment, whatever the "figures" may be. Whether, however, a part or all of the integrating cortical processes are performed in the striate area or in other cortical areas surrounding the striate area, is not feasible to decide here. The most that can be said is that certain structures of the striate area (see Ramón y Cajal, 1909-11, 2, p. 599) suggest that the striate area is itself to some degree involved in this process of integration. Other structural features, however, lead to the conclusion that the area peri-parastriate plays in this process an important and perhaps the main rôle. This assumption is supported by the existence of innumerable fine association fibers springing from the striate area proper and terminating in the neighboring segments of the peri-parastriate area (field 18 and 19 of Brodmann). Yet the preference for certain directions of part of these association fibers, as shown in Experiment XIV, figures 25, 86-94,

¹⁵We are even more forced to accept such a conclusion, since there are no "intercalated" or other "associative" neurons in the external geniculate body, as Experiment V-D and V-E prove.

speaks for a certain preservation of "spatial" relations even beyond the striate area.

That a fixed projection of the retina upon the geniculate body exists has been shown by the experiments of Brouwer-Zeeman and of Overbosch. The work of Overbosch especially demonstrates a surprisingly sharp projection of small retinal segments upon small segments of the external geniculate body in the cat. Less definiteness in projection in the corresponding portions of the visual system can hardly be expected in primates. These studies together with those of Minkowski (1913, 1914), Rönne (1914), Putnam, Brouwer, Heuven, *et al.*, and with the present investigations besides numberless clinical observations, definitely prove the essence of Henschen's and Wilbrand's conception of the organization of the entire afferent visual system according to the "principle of localization." If there are statements contradictory to this view it is now defensible to regard them as surely owing to errors in observation, technique, or interpretation.

Still another result follows from our statements. Since it has been found that the striate area alone and no other region of the hemisphere is the terminal cortical area of the central visual path, it is logical to conclude that all cortico-petal visual impulses will reach the striate area no matter what their special quality is. Thus various color impulses will also enter the striate area and not perhaps a separate cytoarchitectural area outside it. Moreover, because each small segment or "elementary unit" of the visual cortex has its own independent afferent connection with one, single, independent, peripheral "receptor unit" in the retina, each such cortical unit must be capable of reacting to all forms of light stimuli. In other words, each of the elementary visual units including their correlated cortical units, the latter composing the "mosaic" of the visual cortex, will respond to all differences in the length and in the number of light waves. Since all receptive, conducting, and cortical elementary units are equally organized, the response to equal stimuli will be the same. The unequal combination of stimuli will necessarily produce an unequal response of cortical units. But such an equivalent organization exists, it must be assumed, only in a portion of the visual system, in that which corresponds to the macula lutea and probably also to that of its next proximity. The remaining portion corresponding to the extramacular retina, less perfectly organized, will react to a smaller number of light stimuli, and its "spatial" discrimination will be less efficient. But taking a given small portion of that extramacular visual system,

a similar composition of small, equally organized, though less perfect, units must be assumed here, too.

Besides the light stimuli which serve as the material for the higher, "psychic" processes in vision, and which preponderantly use the macular portion of the visual system and enter the macular cortex, other stimuli from the "peripheral" extramacular retina, serving primarily for reflex acts, reach the striate cortex. Since the "peripheral" segments of the retinae are in connection by their own centripetal fibers with the extramacular portion of the striate area, it is the latter which preponderantly serve for the reflex acts of the visuo-motor apparatus.

As regards the relation of fibers of the visual path which conduct crossed and non-crossed impulses, the present experiments lead to the acceptance of a most intimate interrelation of both of these fibers within the visual radiation. It is most probable that fiber bundles emerging from small sectors of the cell layers of the external geniculate body corresponding with homonymous points of both retinae soon mingle with one another, forming a single iso- or homodynamic fiber bundle terminating in a single segment of the visual projection cortex. This, of course, is to be accepted only for those portions used together in the binocular act of vision.

As is apparent from the above statements, the conclusions derived from the present experimental study are decidedly "localistic" both in the main lines, and in all details. With a few exceptions my views are identical with those of the modern "localists" who formed their conceptions mainly upon pathological experience.

With confirmation of the existence of a strictly "spatial" organization of the entire visual system from the retina to the visual cortex our task may be considered as fulfilled. Yet it would be unfair by silence to admit the imputation that all problems of the finer organization and function of the visual apparatus have been solved herewith. To undertake further steps in the explanation of the physiology and psychology of the vision by structures would, however, mean in the present state of our knowledge a departure from the firm ground of positive facts and an ascension into the uncertain sphere of uncontrollable hypothesis and speculation. It is for this reason that I would ask the reader to regard the following statements as mere suggestions.

The fundamental enlightenment derived from the works of Wilbrand, Henschen, Minkowski, Brouwer-Zeeman, Oberbosch, Heuven, and from the present investigations is that the organization of the afferent visual system renders possible an isolated reception, conduc-

tion, and transmission of individual light stimuli to the cortex of the great hemispheres. These studies do not allow any other conception of the fundamental work of the visual system than a faithful transmission of retinal "figures" upon the visual cortex. Yet some modern investigations, notably those of the "Gestalt" psychologists (Poppelreuter, Koffka, Köhler, *et al.*), demand a supplementing of the above conception. As these studies claim, the impression and the image of an external object is not a mere aggregation or a mosaic of small, independent, individual stimuli coming to a fusion somewhere in the central organ, but is a "total" psycho-biological phenomenon, a "figure" ("Gestalt" or "Form" of the German authors) with a meaning of its own. Each figure or configuration is at once in its totality recognized as such and not by a gradual additive process of a number of small individual stimulations. As a particular example a triangle, or a quadrangle, or a circle is under certain circumstances immediately and completely recognized; or a complete circle may be seen though a part of the circle (object) may not exist (the missing part corresponding to the blind halves of the field of vision, as for example in cases of complete homonymous hemianopsia). By some yet unknown "totalizing" and "simplifying" central process, the immediate reception of "whole" forms or "figures," and the comparison of various sizes and shapes would, due to some innate tendency of the central organ to create simple, finished, or "closed," forms or figures, be achieved regardless of the previous experiences. Without further questioning the correctness of all points of the "configuration doctrine" ("Gestalt"-psychology), especially its denying of the "isolation" of reception and conduction of individual stimuli (compare the above lines), it could be asked in what way and by what nervous mechanisms that "totalization," "completion" and "rectification," and in the cases of optic illusions, the distortion of the figures is accomplished. For any casual explanation of these phenomena, the structures, or at least the spot or level in the visual system, must be determined. It seems on the one hand that for the genesis of the above mentioned phenomena, the strictly "spatial" organization of the visual system is an indispensable requirement, since no "figures" whatever can be imagined in a system organized homogeneously and working as a "whole." But this alone is evidently not sufficient. Side by side with the principle of "isolation" and "localization" another principle must be postulated, a mechanism by which the acts of "totalization" and "completion" are performed. Whenever a "closed" or a definite form is perceived, or whenever a "gap" in perception

arises, the special and additional structural and functional arrangements spring in and complete the images till they achieve complete, definite forms. The question arises as to where these mechanisms are and what they are. And here our positive knowledge is utterly lacking. This state of affairs is only natural. The investigation of the visual system has until recently been one of merely settling comparatively rough problems. A sufficiently reliable basis for the study of the finer and more minute problems was largely absent. The minute structures of the retina, of the external geniculate body, and of the visual cortex were studied in a few instances but mostly for other reasons. Most striking is the absence of careful and exhaustive studies with the help of Golgi's and similar methods. The human retina, especially the fovea centralis remains still an unexplored region. Almost so is the striate area. Special attention must be given here to the possibilities of a minute experimental investigation of the macular cortex and by means of the silver methods. This might, perhaps yield some clues as to the structures underlying the phenomena observed by the Gestalt-psychology, and perhaps help to reconcile both opposing conceptions of "localists" and "dynamists." No less important is the study of the area peri-parastriata under the same aspect (and of other regions of the cerebral cortex). The results of Experiment XIV (figures 25, 86-94), which, however, consider only a part of the existing cortical "relations," that is, medullary intracortical and subcortical association fibers, demonstrate a great wealth of especially subcortical association connections of the macular portion of the striate area with the next neighboring segments of the area peri-parastriata. A certain preference of the fiber directions and hence a certain localization of higher, cortical visual processes is elucidated thereby. But many other association relationships and their significance, the stripe of Vicq d'Azyr for example, and other elements remain unexplained. Thus, while the strictest principle of localization in the afferent portion of the visual system must be accepted as an undeniable fact, intricate intracortical mechanisms of the visual region, in the striate and peri-parastriate areas, might co-exist which have another function, that of integrating the single, individual dynamic "elements" reaching the cortex from the periphery into "whole," "complete" visual images. To disclose the identity of these structures and their minute work remains the task of future investigators.¹⁶

¹⁶ Gurwitsch correctly postulates besides an analyzing apparatus in the visual system another mechanism, which he calls "continuum," whose main function

In the study of the organization of the visual system in the present work as well as in that of most other investigators, only the medullated fibers have been considered. Finer structural relations as they can be revealed by silver impregnation of neuronal branches and offshoots were necessarily disregarded. The medullary fibers of the visual radiation were seen assembled into parallel bundles and terminating in small, circumscribed segments of the visual cortex. The foregoing conclusions were therefore inevitable. Yet the study of the visual structures by means of silver impregnation may explain the finest relations of visual neurones to one another, and to the other cell elements of the cerebral cortex. It may be that such investigations will reveal only a relative "isolation" of conductor units of the visual system and a partial overlapping of the terminal branches of individual fibers in the external geniculate body and in the visual cortex, in a mode similar to that found in the auditory system (see my paper, 1927). The degree of such possible overlapping of teledendra might be different in different portions of the external geniculate body, in the macular, and in the extra-macular cortex. Even if this turns out to be the case, it would not mean a "diffuse" arrangement of the visual system, but special "neighboring relations" of contiguous visual neurons with preservation of the "principle of localization."

6. REMARKS ON THE COMPARATIVE ANATOMY OF THE VISUAL PROJECTION CORTEX

Minkowski (1911, 1913, 1914), in his experiments with dogs and cats established the projection of the upper retinal quadrants upon the anterior half of the striate area and that of the lower retinal quadrants upon the posterior and at the same time lower half of the area striata. The lower quadrants of the fields of vision are, accordingly, represented in lower mammals in the oral, the upper quadrants in the caudal half of the striate area. In previous experiments with cats (1927), I was able to determine the supply of the ventro-caudal half of the striate area by the ventral half of the visual radiation,

would be synthesis. That synthesizing mechanism, the structural basis of the unifying "Gestalt"-processes, must, however, not be imagined as non-neuronal, quasi-immaterial, since the existence of special neurons arranged "diffusely" within the striate (and also peri-parastriate) cortex is not only possible but even probable, as the studies of Ramón y Cajal show. Such special structures perfectly satisfy all postulates of the Gestalt-psychology without recurring to the immaterial "continuum." Further, a search for the mentioned special structures of the visual and other cortical regions does not appear premature, but rather needed now to give a firm morphological foundation to the new psychological demands. (Compare Ramón y Cajal 1911 and 1923.)

while in the same experiments the dorso-anterior half of the visual radiation, supplying the oral half of the striate area, remained uninjured. (The origin of the respective halves of the optic radiation and the loss of function was not considered in that work.) According to Minkowski's investigations, the position of the various cortical visual quadrants would seem to be in disagreement with those found for the primates and for man. If we, however, consider the changes that occurred during phylogenesis and the shifting especially of the oral half of the striate area into a more dorso-posterior position—probably in consequence of a more rapid development of the external parietal and rolandic regions—the analogy between the oral half of the striate area in lower mammals and the upper or dorsal half in primates becomes more apparent. The ventral half of the striate area both in the lower mammals and in primates retains, on the whole, its original position.

The striate area has been delimited by numerous investigators (Brodmann, Campbell, Bolton, Mott, Smith, Mauss, Lenz, Cobb, Economo-Koskinas, Putnam, Alouf, Rose, Popoff; see also Ariens Kappers and Economo) in many mammalian classes with a great degree of accuracy. Its relative position in the hemisphere remains nearly the same through the entire mammalian scale. Owing to the variable development of other regions of the hemisphere and to the variable importance of the visual function in various mammals, the relative position and shape of the striate area show only unessential changes. Its position in primates where it is best developed due to the increased importance of vision is particularly stable. Minkowski (1913), showed in an experimental way the identity of the visual projection cortex and of the striate area in lower mammals. In my earlier experiments with cats (1927), it seemed that a narrow zone immediately surrounding the striate area has also to be assigned to the visual projection cortex. That zone would correspond to the "limes parastriatus gigantopyramidalis" of Economo-Koskinas, but the zone—if it really exists in the cortex of Felidae—must at any rate be very narrow. Then, too, the difficulty of delimiting accurately the striate area in preparations of the cat's brain stained by Marchi has to be considered. For these reasons and considering the results of the present series of experiments with monkeys, we are justified in accepting an exact congruence between the striate area and the actual visual projection cortex for lower mammals also, as found by Minkowski.

CHAPTER XVII

RESULTS OF THE PRESENT INVESTIGATIONS OF THE
VISUAL SYSTEM1. VISUAL RADIATION. BOUNDARIES OF THE VISUAL PROJECTION
CORTEX. CORTICAL TERMINATIONS OF THE
VISUAL AFFERENT FIBERS

The uppermost link of the central visual path, the external geniculocortical or the visual radiation, originates in the external or lateral geniculate body. No evidence was found to show that a portion of the visual radiation might originate either in the lateral nucleus or pulvinar of the thalamus, or in the midbrain (superior colliculus). The visual radiation forms a well definable fiber system, called the external sagittal stratum of the parieto-occipital lobes (H. Sachs). The internal stratum of these lobes is a descending cortico-fugal fiber system terminating in the roof of the midbrain. The tapetum or fiber layer closest to the lateral ventricle is purely a callosal system. However, other fibers mingle with the external sagittal layer, namely: efferent (passing to the internal sagittal layer), callosal (passing to and from the tapetum), and also association fibers. At oral levels through the parieto-occipital lobes the most dorsal portion of the external sagittal layer is formed by the most caudo-dorsal bundles of the somatic sensory (thalamo-cortical) radiation.

From its diencephalic origin up to its cortical termination the visual radiation remains strictly unilateral, no portion of it crossing to the opposite hemisphere through the corpus callosum.

The entire visual radiation is composed of regularly arranged and approximately parallel fiber fascicles. It is a fairly thick fiber sheet or lamina having in its totality the shape of a "fan" with its narrow "handle" at the external geniculate body where its fibers lie closely assembled, and its broad wing at its cortical termination. In cross-sections through the occipital lobe its shape is that of a somewhat deformed crescent or sickle which can be divided into three distinct portions: (*a*) the dorsal, (*b*) the ventral horizontal, and (*c*) the intermediate perpendicular or vertical branch, which connects both horizontal branches. This crescent in its concavity facing medialward embraces (1) the internal sagittal layer, (2) the tapetum, (3) the

posterior horn of the lateral ventricle and (4) the cortex of the fissura calcarina with its subcortical fiber layer (calcar avis).

The visual radiation terminates exclusively in the area striata of Elliot Smith, field 17 of Brodmann or the area OC of Economo-Koskinas (shaded areas in fig. 21; see also fig. 24 and compare with fig. 7). No other portion of the cortex of the parieto-occipital lobes, not even the narrow strip of cortex surrounding the striate area and called "limes parastriatus gigantopyramidalis" (Economo-Koskinas), receives any afferent visual or any other afferent fibers in the brain of the monkey. The limits of the cortex receiving the afferent visual fibers and the boundaries of the striate area discernible by the presence of the stria Gennari or Vicq d'Azyr are everywhere identical. This was especially striking in sections showing portions of the striate cortex (marked with number 17 in fig. 76) alternating with portions of the parastriate area, Brodmann's area 18 (marked with number 18 in the same figure). Here the degenerated visual fibers enter only those portions of cortex where the stria Gennari or Vicq d'Azyr is visible, leaving other portions of the cortex entirely free. When still in the subcortical white substance the degenerated fiber bundles keep close along the striate cortex, completely avoiding the other half of the white matter which is close to the non-striate cortex, in a manner similar to that described for the auditory radiation (compare Auditory System).

Taken together, all this means that the visual radiation has a single subcortical origin (external geniculate body) and a single cortical terminal area (area striata); hence in particular the hypothesis of a threefold or a multiple cortical projection of the retina perhaps at spots widely distant and outside the striate area (Déjérine, Monakow, Goldstein, *et al.*) has no anatomical foundation.

The striate area is uniformly supplied with afferent fibers and, accordingly, no special "nuclear or focal zone" comparable to that of the somatic sensory and the auditory cortical projection areas was found. Neither were any small, richly supplied islets of the striate cortex found, separated from each other by narrow zones devoid of afferent visual fibers. Possibly the supply of the macular cortex is somewhat more abundant than that of the perimacular cortex.

In the striate cortex itself the fairly coarse exogenous afferent visual fibers have a more or less oblique course, are mostly distinct from the actual "radiary" bundles, and ascend upward as far as the stria Gennari or Vicq d'Azyr (fig. 65). They must, therefore, be

identical with the fibers of the human striate area found by Ramón y Cajal (1909-11, vol. 2, p. 614) and regarded by him as exogenous afferent fibers originating in the external geniculate body.

2. INTERNAL ORGANIZATION OF THE VISUAL RADIATION

The visual radiation is composed of individual bundles, each having its definite subcortical origin, course, and cortical termination. Neither mixing nor diffuse spreading of the fibers belonging to different though neighboring bundles, nor appreciable overlapping of the territories of the individual bundles, is discernible either during their course or at their cortical termination. The small segments of the striate cortex supplied by individual bundles or segments of the visual radiation are clearly delimitable and even have sharp, linear boundaries. The shape of such cortical segments is triangular or approximately so. The shape, however, varies according to the region. In the *fissura calcarina* the triangles are narrow and lie parallel to the fissure, with their lateral side exactly parallel to the floor of the fissure. The sharp wedge of such a triangle is turned oralward, toward the splenium of the corpus callosum, that is, it lies at the rostral beginning of the striate area where that area occupies only a small portion of the floor of the fissure. As the striate cortex becomes larger toward the occipital pole, extending in the direction of the brim of the lips of the fissure, the extent of these triangles also becomes larger. Over the occipital pole, and, in the monkey, over the occipital operculum the triangles thus supplied are of more compact form, comparable to the calotte of a ball. Here the triangles remind one of the triangular scotomata of the "central" portion of the visual fields; this would indicate a subcortical rather than a cortical origin of these scotomata.

The mutual arrangement of bundles or sectors of the visual radiation drawn from the present investigations is as follows (figs. 22 and 23):

The dorsal horizontal branch has its exclusive origin in the internal segment of the external geniculate body, closest to the thalamus, and terminates exclusively in the upper lip of the *fissura calcarina*, where it descends by bending around the dorsal corner of the posterior horn of the lateral ventricle. That branch remains dorsal during its entire course, forming the dorsal "rib" of the fiber "fan" of the visual radiation. Its course is, therefore, comparable to that of a spiral slowly

ascending dorsally as it approaches the occipital lobe and turning at the same time gradually medialward before it reaches the upper lip of the calcarine fissure. No fibers belonging to the dorsal branch enter the ventral lip of the calcarine fissure or any other portion of the visual cortex.

The ventral horizontal branch originates from the external segment of the external geniculate body; it terminates in the lower lip of the fissura calcarina. It reaches this lip by turning spirally below the lateral ventricle, in a manner similar to that described for the dorsal horizontal branch, though in the reverse direction. This branch forms the ventral "rib" of the fiber "fan" of the visual radiation.

The intermediate vertical or perpendicular branch, representing about half of the entire visual radiation, originates from the large intermediate segment of the external geniculate body. Its course is more direct in the sagittal-longitudinal direction. It has an "axial" position in the visual fiber fan with respect to both horizontal branches which remain "peripheral." The vertical branch supplies the pole of the occipital lobe and, in the monkey, the so-called occipital operculum covering the convex face of the occipital lobe (*Oo* in figs. 21 and 24). The dorsal half of the vertical branch supplies the dorsal half of the occipital pole and of the occipital operculum above the sulcus occipitalis superior or sulcus calcarinus externus of Cunningham-Smith (*Sos* in figs. 21 and 24), while its ventral half supplies the ventral half of the pole and of the operculum below the sulcus.

3. PROJECTION OF THE RETINA UPON THE VISUAL RADIATION AND UPON THE CEREBRAL CORTEX. FUNCTION AND DISTURBANCES OF THE VISUAL RADIATION AND OF THE VISUAL PROJECTION CORTEX.

By utilizing the experiments of Brouwer and Zeeman on the projection of various quadrants of the "peripheral" retina and of the macula upon the external geniculate body in the brain of the monkey, in connection with the arrangement of definite portions of the visual radiation and their relations to definite portions of the striate area as found in the present experiments, the following conclusions in respect to the projection of the retina upon the cerebral cortex may be reached (figs. 22 and 23):

The upper extramacular quadrants of both homonymous hemiretinae have their subcortical representation in the internal segment

of the external geniculate body and in the upper horizontal branch of the visual radiation, and their cortical representation in the upper lip of the fissura calcarina. These correspond with the lower homonymous quadrants of both visual fields, including the lower half of the monocular crescent but excluding the macular portions.

The lower extramacular quadrants of both homonymous hemiretinae have their subcortical representation in the external segment of the external geniculate body and in the lower horizontal branch of the visual radiation, and their cortical representation in the lower lip of the fissura calcarina. These correspond with the upper homonymous quadrants of the visual fields, including the upper half of the monocular temporal crescent but excluding the macular portions.

The homonymous halves of both maculae have their subcortical representation in the large intermediate segment of the external geniculate body and in the intermediate vertical or perpendicular branch of the visual radiation interposed between both extramacular horizontal branches, and have their cortical representation in the pole and (in the monkey) in the operculum of the occipital lobe (*Oo* in figs. 21 and 24). Here the upper homonymous quadrants of both hemimaculae (lower homonymous quadrants of the macular portions of the visual fields) are localized in the upper half of the vertical branch, closer to the upper horizontal branch, and in the upper half of the occipital pole and operculum. The lower homonymous quadrants of both hemimaculae (upper homonymous quadrants of the macular portions of the visual fields) are localized in the lower half of the vertical branch, closer to the lower horizontal branch, and in the lower half of the occipital pole and operculum.

The arrangement of the segments or quadrants of the homonymous hemiretinae as projected into the visual cortex is, therefore, as follows (fig. 23):

The monocular portion of the crossed retina, the so-called temporal sickle or crescent, has its cortical representation in the anterior portion of the fissura calcarina nearer to the splenium of the corpus callosum. Its shape is that of a crescent with both horns turned occipitalward, one in the upper lip, the other in the lower lip.

Behind and partly embraced by it, is the projection zone of the binocular extramacular homonymous quadrants, likewise approximately crescent shaped. This zone, in the brain of the monkey, covers the inner face of the occipital lobe, immediately behind the ascending and descending branches of the calcarine fissure (lower figure in figs. 21 and 24).

Beginning at the occipital pole and, in the monkey, covering the extensive convex face of the occipital lobe, the so-called occipital operculum, as far oralward as the striate cortex extends, is the representation of both homonymous hemimaculae (*Oo* in figs 21 and 24).

The conception of a wide, "diffuse," and perhaps multilocular cortical representation of macula which may also be projected outside the striata area finds no support in the present findings. The macular cortex is the large posterior or caudal portion of the striate area, beyond which it does not extend; it is separate and distinct from the remainder where the primacular portions of the retinae are represented.

The horizontal meridian dividing the upper from the lower extramacular quadrants of the homonymous halves of the retinae corresponds with a line stretching longitudinally along the floor of the calcarine fissure. Its caudal continuation, encircling the occipital pole and then turning again oralward across the external face of the occipital lobe toward approximately the midpoint of the sulcus simialis, is the horizontal meridian dividing the upper halves of both homonymous hemimaculae from the lower halves (vertical lines terminating at *x* and *y* in fig. 23). In the brain of the monkey a shallow sulcus, sulcus occipitalis superior or sulcus calcarinus externus of Cunningham-Smith (*Sos* in fig. 21), might well correspond with the horizontal meridian of both homonymous hemimaculae. A somewhat larger depression or notch at its anterior end might be compared with the cortical representation of the fovea centralis of the macula lutea ("fovea centralis corticalis"), since in the vicinity of this spot the projection of the points of fixation (marked by letter *x* and *y* in fig. 23) must be localized. The vertical line dividing the right and left halves of both maculae is, in the monkey's brain, identical with the anterior boundary of the striate cortex covering the convex face of the occipital lobe, and is fairly parallel with the sulcus simialis (*Ss* in fig. 21). In the human brain this line is usually much closer to the occipital pole, forming the postero-lateral or posterior boundary of the striate area.

Since the entire central visual path above its diencephalic origin is strictly unilateral (as was also found true of the somatic sensory and auditory radiations), a double or bilateral representation of each complete macula in both hemispheres cannot be accepted. Each macula is projected upon both hemispheres, but only in like fashion as the binocular primacular portions of the retinae; i.e., each vertical

half of each macula is projected upon another hemisphere. In other words, each macular cortex represents homonymous halves of both maculae. The sparing of "central" or macular vision in cases of hemianopsia is due to the sheltered position both of the macular cortex and of the macular portion of the visual radiation and to the peculiar arrangement of the "peripheral" and macular bundles in the visual radiation, and also probably to the peculiar blood supply of the calcarine fissure.

4. ORGANIZATION AND FUNCTION OF THE VISUAL SYSTEM IN GENERAL

The entire afferent visual system in primates from its beginning in the retina to its cortical termination is a definite anatomical and functional entity organized "spatially," that is, according to the "principle of localization." In the peripheral portion of the visual system from the retina to the external geniculate body (and also in the superior colliculus of the midbrain) this was shown in an experimental way by Brouwer and Zeeman, and by Overbosch. In the central portion of the visual system, from the external geniculate body to the cortex, the same principle has been demonstrated by experimental, clinical, and pathological studies of Wilbrand, Henschen, Minkowski, A. Meyer, Uhthoff, Lenz, Saenger, Wilbrand-Saenger, Axenfeld, Brouwer, Marie-Chatelin, Holmes-Lister, Holmes, Souques-Odier, Best, Putnam, Heuven, and many other investigators, and is confirmed by the present experiments. It seems, therefore, that there is no longer reason for continued adherence to the old view of a three-fold subcortical origin of the visual radiation and no ground whatever to support the hypothesis of a multiple or "diffuse" projection of the retina and especially of the macula upon a wide region of the cerebral cortex. The relation of the afferent visual path to the cortex is quite definite, and there is but one cortical area which receives direct visual impulses from the peripheral receptor organ. Besides this "gross" relation of the afferent visual path to the cerebral cortex which is decidedly localistic, the same strict localistic principle has been found here to hold for the finer, internal organization of the visual radiation and for its minute relation to the visual cortex. This seems to settle the long dispute about whether there is a fixed, geometric projection of the retina upon the cortex or whether the retina is projected in an unstable or a "diffuse" manner: the decision favors the first view. In general this means that to each minute morpho-physiological unit

of the retina there corresponds a definite, fixed, small segment in the visual cortex (in each hemisphere for homonymous units of both hemiretinae in so far as the binocular portions of the retinae are concerned). But the individual segments of the cortical bi-retina or the quadrants of the visual fields when projected upon the cortex appear somewhat displaced in their mutual relations. The same is observable in the visual radiation and in the external geniculate body though this displacement may in large part be more apparent than real. That which appears to be strictly preserved in the entire visual system from the retina up to the striate area, is the matter of the finer mutual relations of the individual neurons and neuron groups.

Such a conception of the visual system, deduced from the present investigation, yields further implications of consequence to physiology, psychology, and pathology. The striate area is the only "gateway" for visual impulses to the cerebral cortex; therefore all these impulses regardless of their special form or quality must first reach the striate cortex, whence they are distributed to other cortical areas. The view that extensive regions of the hemisphere or even the entire cerebral cortex might in some way or other be concerned with vision, perhaps even with the more primitive, receptive component of that function, has no anatomical foundation.

The further course of visual impulses from the striate area to the surrounding areas also shows a certain regularity and cannot be described as "diffuse." As demonstrated by one of the present experiments (fig. 25, 86-94), involving small injuries strictly limited to the striate cortex, the very numerous and delicate association fibers arising here disperse themselves only in part in a "diffuse" way to the neighboring portions of the striate cortex itself, the majority entering a definite segment of the area peri-parastriata of Elliot Smith or fields 18 and 19 of Brodmann and not reaching other areas of the hemisphere. This points unmistakably toward the existence of a certain localization even in the further spreading of the visual impulses in the hemispheres as supposed by Henschen, and corroborates the supposition of Flechsig that after entering the cortex of the hemisphere the visual impulses do not spread immediately over a great region but first go to the area periparastriata surrounding the area striata, thence diffusing over other more distant areas (see also my papers, 1926, 1927). This leads to the following preliminary conclusions regarding the principles dominating the various connections of the visual projection cortex. The first of these is the strict localistic principle

according to which a "mathematical projection" of the retina upon the cerebral cortex is achieved, the same principle applying also to a part of the further, subcortical association connections of the visual projection cortex with the surrounding non-projection areas of the occipito-parietal lobes. The second principle (or principles), entirely insecure, as yet, possibly coexisting with the first, postulates the existence of short intracortical and subcortical neurons, mechanisms which are responsible for the unity of subjective psycho-visual experiences. (Nothing definite about this minute integrative system can be said at the present time since, beyond a few hints given by Ramón y Cajal, no investigations concerning it have been made; the necessity of postulating side by side with the "localized" structures others lacking the definiteness and specificity or possessing these in a small degree only, particularly within the cerebral cortex, is stressed by Lashley and by Gurwitsch.)

PART IV
GENERAL CONSIDERATIONS

CHAPTER XVIII

GENERAL CONSIDERATIONS OF THE RELATION OF THE AFFERENT PATHS TO THE CEREBRAL CORTEX

It may be of interest to consider the general results of the present investigation of the three main afferent paths of the cerebral cortex and their terminal areas as recorded in the foregoing pages. Clearly the gross relation of all three paths investigated, somatic sensory, auditory, and visual, to the forebrain cortex is definite and constant. Each path is a discrete anatomical and functional entity, distinct, though not entirely separated (anatomically), from other fiber systems; each has its own relationship to a circumscribed cortical locality and its own specific function. Of the three cortical areas wherein these afferent paths terminate (the projection areas or "gateways," the "primary sensory spheres" of Flechsig) and through which the peripheral impulses reach the cortex, the area striata (visual) is sharply delimited structurally, the somatic sensory and auditory areas somewhat less so. These three projection areas appear separated from one another partly by narrow, partly by fairly broad, intercalated cortical zones seemingly void of an afferent fiber supply (fig. 24). Between the somatic sensory and the acoustic projection areas there is a more intimate relationship, both these fields being close together. This fact is, of course, in accord with the view that the auditory (that is, cochlear) system is phylogenetically a derivative of the original common cutaneous system. Between the somatic sensory region and the striate area the intermediate cortex, corresponding in the brain of the monkey with Brodmann's fields, 18 and 19, and perhaps with a part of field 7, is a relatively narrow zone which appears to receive no afferent fibers; this zone is much more extensive between the auditory and the visual projection areas, comprising areas 18, 19, 20, 21 and a large portion of area 22 (compare fig. 24 with fig. 7). It is significant that even in the lower primates considerable portions of the cerebral cortex seem to lack afferent fibers. In this respect the present investigation does not support the belief, shared by many modern neurologists, that all regions of the cerebral cortex (regardless of whether or not they are projectional in the ordinary sense,

that is, receptive and motor areas), receive afferent fibers from sub-cortical nuclei (though they grant that the fibers reaching the various regions may vary somewhat, for example in number). In such a view the distinction between the true projection areas and regions and the intercalated association areas and regions would almost or even wholly

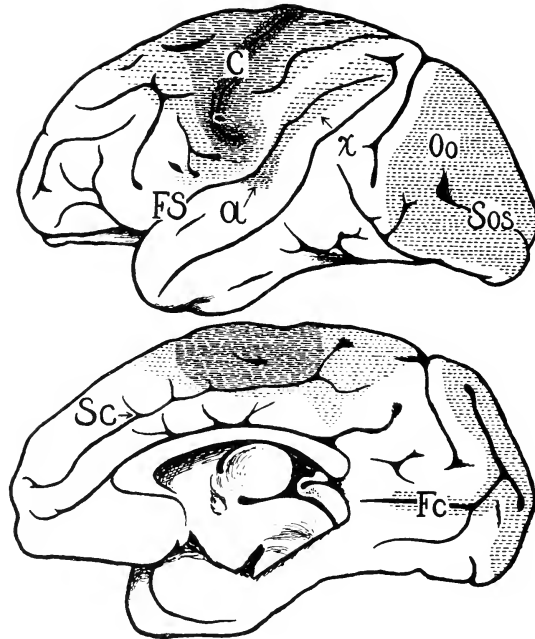


Fig. 24. A diagram summarizing the results of the present experiments on the location and the extent of the three projection areas or regions of the cerebral cortex in the monkey (shaded areas). Upper figure shows the lateral face, the lower figure the medial face of the hemisphere. Sulcus centralis (*C*) with the somatic sensory region in front and behind it. Sylvian fissure (*FS*) with the auditory region (small deeply shaded area *a*) and the projection area of unknown significance along the posterior extremity of that fissure (larger lightly shaded area *x*). Operculum occipitale (*Oo*) behind the sulcus simialis showing the extent of the visual projection area over the external face of the occipital lobe. Fissura calcarina (*Fc*), where the visual projection cortex remains hidden along its horizontal undivided branch. Sulcus cinguli (*Sc*), sulcus occipitalis superior or sulcus calcarinus externus of Cunningham-Smith (*Sos*). (Compare with fig. 7.)

disappear. On the contrary, the present investigation points to a division of the cerebral cortex into receptor fields and intercalated or association areas or regions, approaching in this respect the conception

of Flechsig, supported by Henschen and a number of other neurologists, though their conceptions must be modified somewhat. There is another related question which must, however, be settled by physiological experiments and by clinical studies. Are the projection areas to be regarded exclusively as "gateways" of the cerebral cortex for the incoming impulses, comparable to the switchboard of a telephone station, as claimed by Flechsig and Henschen, or, do they participate likewise in higher integrative processes, as assumed by other neurologists (Niessl von Mayendorf), thus depriving the intercalated regions of the exclusive monopoly of these higher processes? This problem exceeds the scope of the present treatise and will be dealt with in the future after the various association and other connections of the established cytoarchitectural regions have been analyzed.¹ On the other hand, at least some of the intercalated association regions of the hemisphere do not appear to be concerned exclusively with higher processes, since they have subcortical connections of their own, although, so far as ascertained, these are efferent tracts. Thus the area peri-parastriata, for example, stimulation of which results in various eye movements (Bárányi-Vogt, Foerster, 1929²), is the place of origin of the occipital cortico-mesencephalic tract (Experiment XV), while the existence of a similar efferent tract is doubtful in the case of the striate area proper (Experiment XIV, figs. 87-94) though, according to Flechsig's formula such efferent tracts should descend from each receptor area of the hemisphere, and actually do exist both in the precentral and in the postcentral cortex as demonstrated by other experiments of mine involving small injuries strictly limited in some cases to the precentral, in others to the postcentral region (Experiments VI, VII, VIII, figs. 77, 78, 79, 80, 81). As shown in the preceding pages, not only is the principle of localization thoroughly valid with respect to the "gross" relationship to the cerebral cortex of the three afferent paths investigated and to their several functions, but, as demonstrated above, the same principle obtains in the internal organization of all three afferent paths, being most clearly expressed

¹ Compare the remarkable experiments of Foerster (1929) and Foerster-Penfield who electrically stimulated the area striata and the area peri-parastriata in conscious human subjects. (Compare footnote, p. 217.)

² In Foerster's recent experiments in man no eye-movements resulted if the striate area (field 17) was stimulated alone, which had been obtained when the stimulus was applied to the peri-parastriate area (fields 18-19). Biemond found in experiments with monkeys fibers descending from the striate area to the external geniculate body and to the superior colliculus. It is, however, apparent that these fibers arise from areas 18 and 19, since in all experiments of Biemond these areas were partially damaged.

in the visual system; this knowledge is derived partly from the particularly careful study of the internal organization of the visual system in this work. The same principle, however, must not necessarily be considered valid for other afferent systems (olfactory, gustatory), where, in accordance with a different, non-spatial character of their stimuli and impulses, an entirely different architectural and functional principle (or principles) might conceivably exist. (Compare Ramón y Cajal, 1911; Herrick, 1924; Börnstein, 1928; see following chapter.)

Although in view of the results of the present experiments it is necessary to extend the boundaries of the somato-sensory and of the auditory projection cortex beyond the limits determined by the myelogenetic method of Flechsig and by students of cortical cytoarchitecture—though confirming entirely Flechsig's and Henschen's boundaries of the visual projection cortex by demonstrating its identity with the striate area—nevertheless it appears justifiable to distinguish those cortical regions or areas receiving direct impulses from sub-cortical regions (that is, from the peripheral receptor organs) from other areas and regions for which no afferent fibers were found. In distinguishing between the "projection fields" and the "intercalated or association regions" the qualifications and modifications mentioned above must, however, be kept in mind. What appears to be the essence of Flechsig's conception, however, seems to be confirmed by the present experiments, namely, that the entire cerebral cortex does not stand in connection with the afferent paths, but that only some cortical areas or regions possess such connections, these areas having a definite location, shape, and extent and a specific function. Through these "gateways" specific impulses from the surrounding external world, as well as from the internal organs of the body, enter the cortical sphere, there to undergo the most varied processes of combination and integration. The following question must form the subject of further studies: By what connections are the impulses reaching the projection areas distributed to other areas and regions, especially to the intercalated regions, and by what mechanisms are the different impulses integrated into new composite forms of neurodynamic phenomena? In other words, how are we to interpret anatomically the function of the projection and association areas, especially that of the temporo-parietal and frontal regions?

At any rate, the present experiments corroborate the belief in an unequal, diversified representation of various functions in different

portions of the cerebral cortex, and in the existence of a "spatial" internal organization of the somatic sensory, auditory, and visual afferent paths; they stand in contrast to the attempts to restore in some form or other the old doctrine of the functional equivalence, or omnivalence of the entire cerebral cortex.

Without a minute and extensive discussion, and without far reaching conclusions, it may be stated in general terms that the results of this study indicate that the whole question of the anatomical organization of the brain and of its function, is largely one of localization, although our imperfect knowledge makes this principle in many respects appear obscure. The idea of unequal local function of the nervous system in general, and of the cerebral cortex in particular, is as old as modern brain research. During the last hundred years it has undergone considerable modification in details, due to development in other branches of natural science and to the accumulation of data on the anatomy, physiology, and pathology of the brain. Naturally, in its early form the localistic conception was "naïve," which made it an easy task for its opponents to show its weak points. But the opposite doctrine, that of an equal or equivalent significance of the whole cerebral cortex has all the characteristics of another extreme, even in its milder, modern form (though some modern authors seem to have returned to the ill-founded integral conception of the cortical equivalence of Flourens and Goltz). In reaction against too simple and rigid a localistic explanation of higher mental and related processes many modern neurologists maintain that in all major activities the greater part of the cerebral cortex or even the entire cerebrum, perhaps together with the whole somatic apparatus, is nearly always involved. Although in some sense acceptable,³ this view undoubtedly over-emphasizes and generalizes a single aspect of the brain's activity; for, the same type of explanation could as well be applied to somatic organs and systems, which indisputably have distinctive functions though they are parts of the whole organism and always collaborate more or less in its activities. As Vogt pointed out, the localistic conception is capable of satisfying the demand that it explain the highly complex nervous processes (Vogt, 1919, p. 443). An analytic attack, namely, an attempt to identify and distinguish the different morphological parts and their special functions, appears to be a necessary preliminary before reconstruction of the archi-

³ See especially the experiments of Lashley showing the participation of large parts of the cerebral cortex in the formation of some of the complex habits.

tectural and functional plan of the whole nervous apparatus, especially of the cortex, can profitably be undertaken. From this point of view the first task is to establish the relationship between certain nervous functions and certain parts of the cortex. In view of the striking local variation in cortical structure, the various cortical localities would be expected a priori to be responsible for some kind of primitive or elementary neurodynamic processes, some "partial functions," different in different localities, the acts expressive of these being

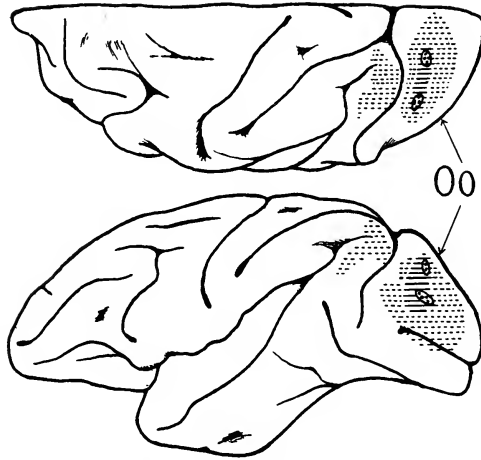


Fig. 25. Experiment XIV. A diagram showing the left hemisphere from above (upper figure) and its side view (lower figure) with two small strictly cortical lesions (small dotted areas) of the occipital operculum (*Oo*). The shaded area over the occipital operculum is the portion of the striate area; the shaded area in front of the simian sulcus is the portion of the angular convolution supplied by the association fibers originating from the lesions. (Compare figs. 86-94.)

usually simplified summaries of combinations of a higher, composite order. At present the difficulties in solving the problem of mental-material relations appear, on the whole, to reside less in the sphere of morphology than in the definition of the localizable elementary cortical processes. Psychological methods of investigating the manifestations of mental and associated phenomena are comparatively crude, and clinical methods are even more so, dealing as they do, mostly with composite symbols to which can hardly be assigned their adequate morpho-dynamic parallels or correlates in restricted, narrow localities

and definite structures. Nevertheless, some of the indisputably cortical performances so far disclosed are localized in small portions of the cortex. This is the case with certain functions of the projection regions and with effector functions of the precentral and postcentral regions, and of their corresponding afferent and efferent fiber systems. For the precentral and postcentral regions this was demonstrated by the physiological-histological experiments of Vogt (1919, Mitt. 4, p. 399). The same has been ascertained for the receptor function of the postcentral region by Cushing (1909), Valkenburg (1914), Foerster (1927), Mankowski (1920), Foerster-Penfield, and a great number of other investigators, mostly clinicians (see bibliography), for the visual system including the striate area by Wilbrand, Henschen, Minkowski, Brouwer-Zeeman, Overbosch, Putnam, Foerster, Brouwer, Heuven, Foerster-Penfield, R. A. Pfeifer 1930, and many others; and for the auditory system by Held-Kleinknecht, Quensel-Pfeifer, R. A. Pfeifer, Kleist, Lorente de N6 *et al.* My previous and present investigations justify admission of the existence of differences in functional significance of various specific afferent paths of the cerebral cortex, and even of the individual small neuronie units composing each of the somatic sensory, auditory, and the visual systems together with their respective cortical terminal areas. Moreover, it appears logical as a next step to admit the existence of some kind of localization of "higher" activities in the chain or sequence of events interposed between initial afferent processes and final efferent acts. (This does not necessarily preclude the co-existence of other paths with ill-defined and more labile connections which would meet the requirements of the Gestalt psychologists and would be in accord with Lashley's areal "equipotentiality"; unfortunately these integrative mechanisms can not at present be identified.)⁴ Nor does it seem possible to avoid such

⁴ To explain these two apparently contradictory statements we may use as an example the visual projection cortex (striate area, field 17), especially its macular portion. As is evident from the present experiments and other investigations, a very strict or, better expressed, a point-to-point projection of the retina upon the cortex with the corresponding arrangement of afferent fibers can hardly be disputed. Also it cannot be denied that the visual projection cortex participates in a somewhat different way in cortical visual processes than the region immediately contiguous to it. When we consider a far reaching "principle of localization" with respect to the structures and functions of the afferent portion of the visual system, we are struck by the comparatively small size of the main cortical receptor apparatus, that is of the macular cortex, large as this cortex is in the brain of the monkey. This region receives the bulk of the afferent impulses rapidly changing in time. Therefore, it must be concluded that the same cortical apparatus, in this case the macular cortex, is capable of rapid response to practically an unlimited number of stimuli of a most varied kind. Although, according to our conception, the "spatial" arrangement of visual neurons exists and is,

a conclusion, however risky this might appear and difficult to solve, if we consider the advanced structural differentiation of the human cortex as compared with that in lower mammals (consult Brodmann, Ariens Kappers, Herrick, 1926, and Economo-Koskinas). Nevertheless, as previously stated, the difficulty here is not only in discovering special structures, the substrata of particular primitive functions, but also in determining and in defining of those primitive or elementary processes to be localized. Be this as it may, advance in the disentanglement of these intricate problems may be expected from further investigation of the organ of the mind itself and by improved methods of study rather than from elaborate speculation (A good presentation of the problem of localization of "higher" cerebral functions one finds in Isserlin's and in Economo's [1929] papers.)

moreover, a necessary prerequisite for the preservation of the visual "figures" up to the striate area, the latter apparatus, thanks to its organization, is endowed with the ability of reacting in most varied ways. Because of this, the conception of fixed and unalterable relations between individual visual "figures" (and "images" as well) on the one hand, and definite groups of neighboring ganglion cells on the other, as alleged by some localists, does not appear to be appropriate. It appears more probable that in most of the visual receptive (and perceptive) acts, a large number of cortical cells are activated. Some or many of these same cells are involved at a different time in different receptive processes (different combinations of the same cells produce central "figures" totally different from the preceding). This is more probable since in view of the small size of the macular cortex, most of the "figures" produced here will necessarily expand over the greater part or occupy almost the entire macular cortex. A similar property, the ability of the same nervous elements to react to the most varied stimuli, has to be attributed even in a greater degree to the visual association areas (fields 18 and 19, area periparastriata) which have, on the whole, a different function than that of the striate area (field 17). Considering also the small size of the peri-parastriate area in the monkey, it is more appropriate to think that most of the visual and composite "images" are bound to structures distributed over a large part of the mentioned area. (In these speculations the following fact has been taken into consideration: in monkeys, which undoubtedly have a very well developed "visual memory," because of the comparatively small size of the peri-parastriate area which is hardly larger than the striate area, the striate area must also actively participate in the so-called "higher" visual processes, and cannot be a mere "through station" or a "switchboard" for the incoming impulses). That the striate area acts more-or-less in its totality in certain functions has been well demonstrated by Klüver's experiments with monkeys.

CHAPTER XIX

AN ATTEMPT TO EXPLAIN STRUCTURAL FEATURES OF
THE AFFERENT PATHS IN CONNECTION WITH
THEIR FUNCTION AND THEIR BIOLOGICAL
SIGNIFICANCE

To understand the phylogenetic appearance of the afferent paths, to explain their morphological peculiarities and their function, it is indispensable to consider the general biological rôle such systems play in the life of animals. Such a study will give clues as to why certain neurons acquire the ability to receive and conduct special impulses from without, and as to whether the internal organization of the afferent paths stands in some causal relationship to the external stimuli. In the present discussion of these problems our method will be that of pure description and statement of facts with the realization that the real inner causes—physical, chemical, neurodynamic, and so forth, must of necessity, because of lack of data, remain unconsidered.

Undoubtedly the appearance of afferent neuronie complexes with specific functions must be caused by some special external causes, which serve as the creative stimuli. (It must be granted that the inherent properties of protoplasm enable such changes to occur.) It could a priori be expected that the number of afferent paths will approximately correspond to the kinds of the external stimuli. It can also be expected that the nature or form of the physical and chemical agents serving as stimuli will in some way or other be reflected in the inner structures and, therefore, in a special mode of action of special afferent systems. And lastly from the general biological view point, there can be little doubt that each of the afferent paths together with their special peripheral sense organs evolved in the course of phylogenesis will serve its own purpose in the life of the animal regardless of whether a planful purpose was or was not originally intended.

In some sense it can be assumed that every living being or individual stands apart, in opposition to the entire surrounding world. Yet being, nevertheless, a part of that surrounding as long as it exists every individual stands in an incessant interrelationship to its environment, to which it must either adjust itself, or adapt that environment to its own needs, or, most usually, act in both these directions. The

position of every individual in its relationship to surrounding nature is, therefore, usually that of an object and at the same time, that of a subject. External agents act incessantly upon individuals which in turn are provoked to a reaction or to a response. In such a way the action of the environment upon an individual and the reaction of the latter seem to be the essence of life's function. And again, the appropriate reaction of the individual is indispensable for its welfare and even for its very existence. Only by reacting in a suitable way to the external factors can the individual satisfy its inherent urge to maintain its own existence and to continue it by new individuals.

In the higher forms of animals, in Metazoa, the supreme arbiter of the individual in its adjustment to environment is the nervous system. In higher stages of the animal scale, that rôle is chiefly performed by the central nervous system. Yet not only the actual environment outside the individual but the somatic part of its own body appears in some respect as the "external world." Thus the actual surrounding of the individual and in addition the somatic part of its own body both stand in opposition to the central nervous system.

The central nervous system, accordingly, occupies the position of an "Ego" to surrounding objects and also to the somatic part of the individual. That "Ego," or the central nervous system, in the first place the cerebral cortex, is the real subject which must be brought in relationship to the "environment" and to decide upon the reactions to be taken in each of the major changes of situation.

When considering the relation of the individual to outside objects, this is achieved by the external impulses through which the central nervous system gets knowledge about the changes in external conditions. In this phase the individual or the central nervous system plays the rôle of a passive object. The second subsequent act of the central nervous system is its reaction or response, wherein it is an active subject.

From this speculation it appears evident that the task of all afferent systems of neurons is to receive stimuli arising in the environment (without separately considering here those impulses having their origin in various somatic organs) and to convey these stimuli to the central nervous system. Here the decision is made on the mode of reaction. In general terms the task of afferent systems is to bring the individual into various special relationships to the environment and thus to enable its proper orientation.

The relationship of the individual to the environment and to its changing conditions is achieved in lower stages of the animal scale exclusively or preponderantly by an immediate contact with the medium wherein the animal lives. Here it is almost the entire surface of the body of the animal which plays the rôle of the receptive or sensitive surface for the various stimuli. The stimuli to which lower animals react are mostly of a short range, tactual, chemical, and thermic, while others, notably light and sound, play an inferior or negligible rôle. For orientation to these stimuli a "diffuse," poorly specialized nervous system and corresponding primitive receptors suffice. Only gradually certain parts of the nervous system acquire the ability to react to special forms of radiant energy, especially to those whose source lies at a greater distance. To receive, to conduct, and to utilize stimuli arising from the latter forms of radiant energy, special parts of the nervous system are "condensed" from the originally diffuse system into special paths, and special peripheral organs facilitating the reception of the special stimuli are evolved. In connection with this, special small portions of the surface of the body or of the nervous system itself are transformed into highly sensitive receptor surfaces (retina, cochlea, vestibular apparatus, and so forth), containing a greatly increased number of neurons (these changes going hand-in-hand with structural modifications).

Still another fact has to be considered. The increase in the number of neurons itself in the afferent paths and even their structural and chemical perfection without further changes would merely signify facilitation of the reception of stimuli—for instance, increased intensity and other quantitative changes. The properties of stimuli, notably those which could be named "spatial" or "dimensional" would be of no use since the "diffusely" organized afferent paths would always react "in toto" (as for example, the olfactory and gustatory paths). No or little "spatial" or "dimensional" discrimination of external stimuli would in fact be possible. The eminently "spatial" character of visual, auditory, tactile, and vestibular stimuli, being in itself a superior quality, serving for orientation in space, requires evidently an organization of sense organs and of the afferent paths different from that which suffices for the reception of stimuli void of a "spatial" character.

The changes which occurred in some of the highly specialized afferent complexes of neurons and enabled the utilization of the "spatial" properties of certain stimuli might be called the "rearrange-

ment of neurons." This rearrangement of the receptive and conducting neurons, gradually evolved, culminates finally in a peculiar mutual relationship of individual neurons of each of the affected afferent paths, an arrangement which renders possible the reception, conduction, and utilization of stimuli affecting a very reduced portion of the peripheral sensitive surface and involving a small number of neighboring neurons, or even a single neuron. The most perfect example of this in the higher mammals, is the visual system.

In this way, (*a*) by "condensation" and "isolation of neurons" from the originally diffuse nervous system into special "systems" of neurons or afferent paths, and (*b*) by the "rearrangement of neurons" in each of the above mentioned systems with respect to their mutual relation (besides other consequential changes in the central nervous system), the exploitation of the superior "spatial" or "dimensional" properties of certain stimuli is made possible, this utilization being limited only by the absolute size of individual neurons (for example in the fovea centralis of the human retina).

According to this viewpoint it is the rearrangement of afferent neurons which, besides those minute changes in the neuroplasm itself which facilitate its function, signifies and conditions a perfection of highly specialized afferent paths, especially those connected with distance receptors (except the olfactory system). The real causes of this rearrangement, however, are unknown, and it is not my intention at present to go beyond the simple statement of facts. One might consider the tendency of neurons which usually act together to take neighboring positions (compare Ariens Kappers, 1920-21, pp. 70 and 898; see also Bok, 1915, p. 536, Hanström, and Veit); yet this alone would not explain the actual causes of the "isolation" nor the additional hypothesis that neurons not acting together have the ability to separate from one another.

The above mentioned rearrangement of afferent neurons and their adaptation to the spatial or dimensional nature of certain stimuli is variously advanced in different stages of the animal scale and is not equally well expressed in different systems in the same animal. While it is most evident in the visual system in most of the higher animals, especially in mammals and in birds, it is less developed or at any rate, less striking in the somato-sensory and in the auditory systems, being apparently quite absent in the olfactory and in the gustatory systems. Even in one and the same system the "spatial arrangement" of neurons reaches a different degree of perfection in different parts.

Thus in the human somato-sensory system it is best developed in that part conducting epicritic or gnostic tactile impulses, while in the part conducting pain impulses, it remains closer to the original diffuse condition (compare Foerster, 1927). Even in the most highly differentiated system, the visual apparatus of primates, that part corresponding with the "peripheral" portion of the retina is considerably less "spatially" organized than the macular portion. It is significant that even in insects and in some of the lower vertebrates (Chameleo) the visual system already shows striking perfection in the above sense (Ramón y Cajal, Ramón y Cajal y Sánchez, Sánchez y Sánchez).

With the gradual perfection of the afferent systems and their peripheral receptor organs, especially those called "distance receptors" (Sherrington), the "surrounding world" of a given species widens and extends from the immediate vicinity into a larger "world." As long as the nervous system and its receptive and conducting mechanisms are capable of receiving only those stimuli which act by contact or by chemical and other changes, the "world" is very limited in its dimensions and its constituents, other parts of the environment being in fact non-existent. When highly perfected distance receptors, with subsequent change of the nervous apparatus, are evolved, the radius and the complexity of the "world" extends practically beyond any limits and in this measure the appreciation and knowledge of the "world" increases.

The widening of the "world" and the ability to discriminate and utilize a greater number of stimuli arising from it, is doubtless of advantage to the possessor. (To illustrate this one may consider countless observations of the interrelationships of various higher and lower species of mammals living under natural conditions.) By giving them a wider scope and an increased analytic power and in this way facilitating the avoidance of noxious agents, by bringing a greater amount of food into their range, and even by facilitating reproduction, highly perfected distance receptors and "spatially" organized nervous paths would put such a species in many respects in an advantageous position in comparison to species having less developed receptors and conductors. With closer study of natural conditions and of the adaptation of various animal species to these it soon becomes apparent that animals cannot a priori be regarded as adapted to their special surroundings or their "worlds" and are certainly not all equally well adapted. Apparent perfect adaptations are hardly more than appearances, resulting from inadequacy of observation. Such seemingly

static conditions would be comparable to a single picture of a moving film which is, in reality, nothing more than a brief scene of a long process. A "perfect adaptation" of living beings to their special environments can, therefore, be accepted in a restricted sense only. Furthermore, the surrounding "world" of a given species is equally unstable. Other factors forming other different "worlds" intrude incessantly into it, however difficult this may be to detect. Also the "worlds" of different animal species overlap each other. A steady readjustment of individuals and species to new factors is therefore a permanent requirement of life. The success of this readjustment will greatly, though by no means exclusively, depend on the efficiency of their receptor organs and the conductor and other nervous mechanisms, and on more perfect and adequate utilization of stimuli. The better an individual is informed about the happenings in its environment, the better chances it has—*caeteris paribus*—to survive and to preserve its species.

The efficiency of an afferent system and of its receptor mechanisms, will be higher if a more adequate, a more "true," or a more "objective" picture or information about the environment is received. It will be of unsurpassed value if the subjective impression in all details closely corresponds to the external stimuli, that is, to the external objects, if the picture reproduced within the "internal world" of the individual, in the first place in its central organ, is in some sense a mirror image. This can be achieved only if the internal impression contains constituents of stimuli of as many external factors as possible and these in as faithful, mutual relation as exist in the "external world" or in the objects.¹ The efficiency of various afferent systems and of the central organ will, therefore, depend not only on the action of the neuroplasm, on its sensitiveness or susceptibility to stimuli, on the speed of their transmission and so forth, and thus on the radius of the action of the corresponding sense organ, but to a high degree on their ability to "spatially" analyze differently composed external stimuli or sets of these. And it is this latter ability to discriminate small stimuli and to utilize their "spatial" or "local" qualities on which the "faithfulness" or "trueness" of the internally evoked impressions, pictures, or images of the external objects ultimately is based.

¹ We may completely disregard here the "thing-in-itself" of the philosophers and face the world of "practical realities."

Since the stimuli emanating from external objects are for the most part of a complex nature, the ability of an afferent system to create an "objective" impression and to transmit it in such a form to the central organ, to the cerebral cortex for example, will depend first on the ability to "decompose" these complex stimuli into their elementary constituents. That tendency to decompose or to analyze complex external stimuli seems to be the meaning of the perfection of all the higher afferent systems concerned with radiant forms of energy (stimuli). It is the elementary stimuli which when separately received permit the finest and, accordingly, the most adequate judgment of the nature of a certain composite stimulus. The task of the highly perfected sense organs and of their corresponding nervous apparatus seems, in general, to be to bring down the complex external stimuli to their elementary components or to primitive stimuli and to transmit these latter with as little change as possible to the central organ, especially to the cerebral cortex. It is this latter place where the arriving primitive stimuli or at most some simple combinations of these are once more welded together to produce higher composite forms of nervous activity of a very different character. The analytic peripheral nervous process with subsequent central synthesis can be compared with similar processes in digestion. Since the cells of various organs are unable to utilize the nutritive material represented by highly complex molecules, the latter must first be split into simpler chemical units. In such simple form the nutritive material is made suitable for resorption in the alimentary tract, for transport to the places of its utilization and consumption by the cells of the organism. In these latter the process of decomposition can take its further course, or new more complex chemical units are made by a synthetic process.

As to the concrete problem as to how far the organs of the senses, their afferent paths, and perhaps also other parts of the central nervous system exhibit in their architecture a reflection of the physical properties of various external stimuli has only occasionally been mentioned in the preceding chapters. Further statement is likely beyond surmise in the present state of our knowledge.

In the light of the above explanation the various modes and degrees of perfection of the afferent paths (including all finer changes in internal structure and chemism) appear as being due primarily to properties of the external stimuli to which they react. Where the stimuli possess a "spatial" character (light, thermic, and sound waves, gravitation, and similar forms of energy like inertia, and touch)

the receptor organs and their afferent paths when fully developed exhibit a "spatial" arrangement of neurons. In the case of organs and paths dealing with non-localizable forms of stimuli (smell, gustation) a "spatial" arrangement of neurons is absent. (Some of the ideas expounded above are to various degrees expressed here and there in the works of Parsons, Child, Parker, Uexküll, Ariens Kappers, Bok, Herrick, Weizsäcker, Sherrington, Ramón y Cajal, Russel, Monakow, V. Franz, Plate, Darwin, Wallace, Ettliger, Hanström, Tschermak, *et al.*)

CHAPTER XX

REMARKS ON FUTURE INVESTIGATION OF THE
CEREBRAL CORTEX

One of the objects of the present work was to facilitate further investigation. A few points in this connection may be mentioned.

Some modern experimental psychological investigations have apparently yielded results not easy to reconcile with the conception of the striate area as the sole "gateway" of the cerebral cortex for all afferent visual impulses. For practical reasons, in experiments on brightness discrimination, for example, lower mammals have been used almost exclusively. Yet it is well known that the visual system in the higher mammals and in man, though essentially the same, differs considerably from that in lower mammals where the mesencephalic visual mechanisms are better developed (see for example Ramón y Cajal, 1909-11, vol. II, p. 386; Monakow, 1914, p. 127; Ariens Kappers, 1920-21, vol. II, and Herrick, 1926; consider also the well developed mesencephalic visual centers in the rabbit, organized according to the strict localistic principle as found by Overbosch). It appears, therefore, probable that the retention of ability to form the habit of brightness discrimination observed in some of the above mentioned experiments where the striate area was destroyed on both sides, was due rather to the activity of the lower, subcortical visual mechanisms, than to the remainder of the cerebral cortex. Be this as it may, before they are applied to higher mammals and to man, the results derived from the study of the visual function in lower mammals might well be confirmed by experiments upon primates (complete ablation of the striate area on both sides!), and controlled by further experiments on rats, comprising removal of the entire cerebral cortex of both hemispheres with the preservation of the subcortical visual centers.

Furthermore, the contradictory results of various physiological and psycho-physiological experiments involving the removal of certain cortical regions supposedly visual, auditory, or sensory in function are easily explained in view of the present experiments. Only rarely were the corresponding cortical centers actually completely removed or destroyed. Usually a considerable portion of these remained intact and this has led, of course, to erroneous conclusions. (See for

example Ferrier-Turner, Luciani, and S. I. Franz.) Thus in Franz's eight monkeys the striate area was not in a single instance removed completely, nor was the visual radiation interrupted entirely, usually half or even considerably more of the striate area or of the visual radiation remained intact (so far as one can judge from illustrations in Franz' paper). The advantage of experimental anatomical investigation (or, better, of a combined anatomical and physiological procedure) unquestionably lies in the fact that it furnishes reliable data as to the terminal regions of the afferent paths investigated, thus indicating where to operate. By showing the location and the extent of the "primary" or projectional cortical regions of the hemisphere for the somato-sensory, auditory, and visual paths, anatomical investigation affords a sound basis for further research on cortical functions in primates and hence in man; in particular: (1) for investigating the distinctive function of the "gateways" of the cerebral cortex by the isolated removal or destruction of the projection areas or parts of these, of the macular cortex, of the perimacular cortex, of special areas of the precentral, and of the postcentral somatic sensory cortex, of the auditory areas *a* and *x* together and separately, and so forth, on one and on both sides; (2) for studying the nature and the sites of higher integrative and other processes localized in the intercalated regions by isolated removal of parts or of whole regions not directly related to the afferent paths. In the future it must be kept in mind that if complete destruction of the sensory cortex be desired, its "focal or nuclear zone" must also be removed. Furthermore, when investigating special receptor functions of the postcentral or of the precentral areas, the ease with which the "focal zone" of the somatic sensory cortex, as well as its portion of the thalamo-cortical radiation, can be damaged, either from the postcentral or from the precentral convolution, must be taken into consideration. This being true, only the results yielded by refined operative technique followed by a thorough anatomical examination will be accepted as conclusive. What is true for the somatic sensory cortex is valid also for the study of the auditory and of the visual areas. To destroy the auditory projection area the entire ventral wall of the Sylvian fossa as far inward as the inner or vertical wall of that fossa must be removed. (The question, however, remains whether this alone will be enough, since, as stated previously, the function of the area *x* is unknown.) Similarly the visual projection cortex cannot be considered as completely destroyed unless the entire striate area has been removed including the portion buried

in the calcarine fissure. On the other hand it is obvious that areas 18 and 19 as well as areas 20 and 21 and the greater portion of area 22 of Brodmann in the brain of the monkey lie outside the projection fields of the hemisphere and offer us, therefore, the opportunity to study their functions by partial or by complete ablation.¹

New prospects are also opened for the further investigation of the special functions of distinct cytoarchitectural areas in conscious subjects as practiced by Cushing, Krause, Valkenburg, Foerster, Mankowski, and others, as well as for clinical, pathological, and anatomical studies. With respect to the somatic sensory cortex, for example, it will be necessary to bear in mind that the "nuclear or focal zone" of that cortex is completely sunk in the sulcus centralis and does not reach the convexities either of the anterior or of the posterior central convolution.

In conclusion a few words may be permitted concerning general ways and means of experimental brain research. If experimental anatomical, physiological, and psychological research is to shed more light on the mechanisms and the nature of the highest nervous processes in man, this can scarcely be achieved by using lower mammals. In these it is difficult to produce sufficiently localized injuries, confined to definite small portions of the cortex, to certain cytoarchitectural areas or regions, without damaging other areas and the subcortical white mass, or even disturbing the entire brain, not to mention the danger arising from the application of the results obtained with primitive brains to human conditions. The brain of the lower primates is, on the contrary, in its essential features and in its finer structure a simplified replica of the human brain. This fact, together with the comparatively large size of the monkey's brain, makes orientation and the technical aspect of the work more certain and

¹ No less important is a systematic study by areas of the association, callosal, and efferent fiber systems of the cerebral cortex, preferably with the help of Marchi's method. The next task will be a systematic study of finer structures of the cortex with the help of Golgi's and Ramón y Cajal's silver impregnations. Finally, much could be expected from a study of special areas (the striate area in the monkey, for example) with regard to the preservation of "figures" in subcortical centers (the external geniculate body). After producing small, strictly cortical lesions representing various figures, the resulting degenerated portions of the subcortical nuclei should be determined with the help of the Nissl's method (Nissl's "primary irritation"), mapping their extent, shape, and position. The same could also be done with the somato-sensory and auditory cortex by examining the degenerated figures in the thalamus and in the internal geniculate body in a way similar to that applied in our Experiment V-c. (A similar method, though only for a less exact purpose, was applied by Heuven in his recent study of the visual system.)

much more convenient than in lower mammals. Certainly a systematic experimental investigation of all the chief anatomical, physiological, and psychological problems of the brain on a large scale and with a broad view, according to a prearranged plan, using primates, would give results amply compensating the labor, the time, and the expense involved.

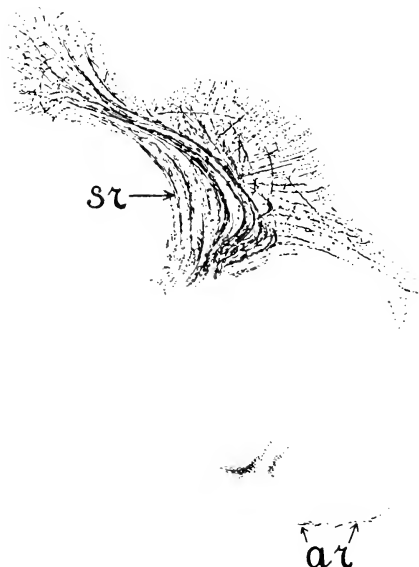


Fig. 26, Experiment I. Somatic sensory thalamo-cortical radiation (*sr*) entering the precentral convolution (*CA*); black lines and dots represent degenerated fibers of the radiation. This portion of the radiation is its anterior or rostral "fan." Its fibers ascend through the anterior limb of the internal capsule, spreading over the entire precentral convolution (its thalamic origin is seen in figs. 28, 29). A portion of the anterior commissure and of the external and extreme capsule is also degenerated. A few degenerated fibers of the auditory radiation (*ar*), the most rostral in the series, are visible in the superior temporal convolution. Sylvian fossa (*FS*), superior temporal sulcus (*St*).

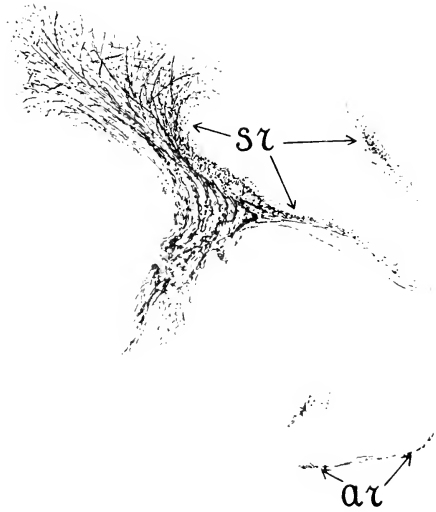


Fig. 27, Experiment I. Somatic sensory (*sr*) and auditory radiation (*ar*) as in the preceding figure except that a portion of the postcentral convolution (*CP*) and the anterior segment of the thalamus (*Th*) appears, while the precentral convolution (*CA*) is decreased in size. Sylvian fossa (*FS*).

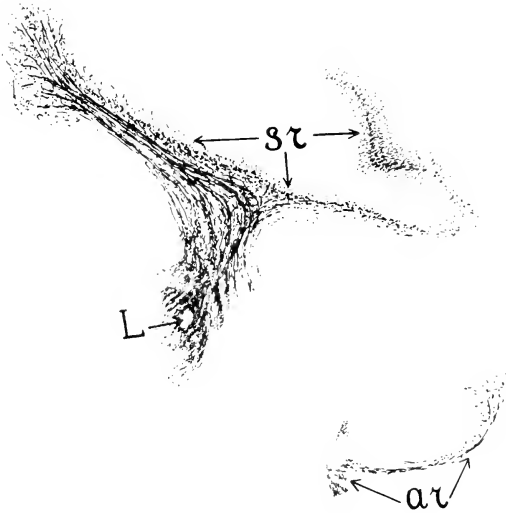


Fig. 28, Experiment I. Somatic sensory radiation (*sr*) containing a greater number of fibers than in the preceding figures. It enters both precentral (*CA*) and postcentral convolution (*CP*) many fibers penetrating into the cortex forming the floor of the sulcus centralis (*C*). The anterior end of the lesion (*L*) in the thalamus (*Th*) appears. The auditory radiation (*ar*) here also contains more fibers and enters the upper lip of the superior temporal convolution (*T₁*) which forms the lower wall of the Sylvian fossa (*FS*). In the external capsule the small degenerated bundle above the auditory radiation belongs to the anterior commissure.

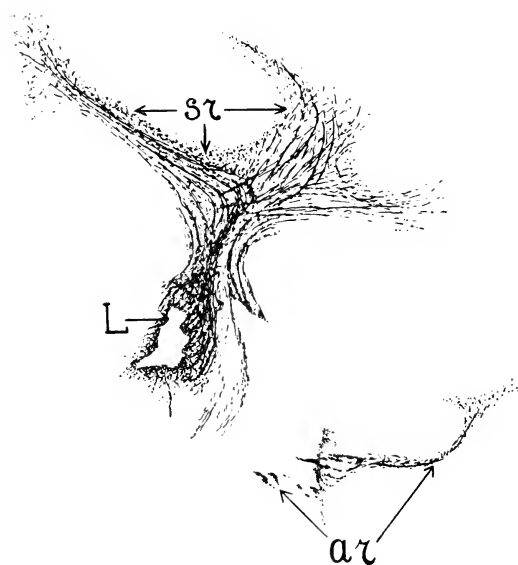


Fig. 29, Experiment I. The degenerated thalamo-cortical radiation (*sr*) emerges from the thalamus (*Th*) where the lateral nucleus was injured (*L* = lesion) without injury to the internal capsule; it ascends toward the precentral (*CA*) and the postcentral convolution (*CP*) and to the cortex lining the central sulcus (*C*). None of these fibers enters the corpus callosum. Bundles of the auditory radiation (*ar*) partly still in the globus pallidus and in the putamen, partly already lateral to the latter nucleus below the ventral "spur" of the claustrum; they enter the superior temporal convolution (*T₁*), reaching the cortex of the ventral wall of the Sylvian fossa (*FS*) exclusively. None of the auditory fibers enters the cortex lining the superior temporal sulcus (*St₁*). The origin of the auditory radiation is seen in figs. 33, 34; its course through the internal capsule in figures 33, 32, 31, 30. (These figures also show bundles of the auditory fibers passing between the islets of the putamen.)

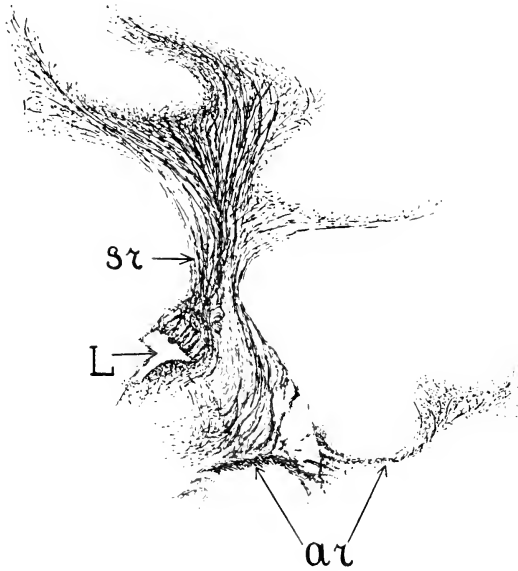


Fig. 30, Experiment I. The degenerated thalamo-cortical and auditory radiations (*sr* and *ar* respectively) as in the preceding figures except that the ventral bundles of the somatic sensory radiation from the ventro-lateral nucleus of the thalamus (their origin visible in fig. 33) are shown here passing through the internal capsule, these fibers being also closest to the auditory radiation. Lesion (*L*) in the dorso-lateral nucleus of the thalamus (*Th*). Note the appearance and position of the auditory radiation in the most ventral portion of the internal capsule immediately above the external geniculate body: a dense bundle of short oblique fiber segments. The acoustic fibers pass through the putamen (the latter here much reduced in size) into the white matter of the superior temporal convolution (*T₁*) where they occupy the upper half of the white matter exclusively and enter the cortex of the lower wall of the Sylvian fossa (*FS*). No acoustic fibers whatever reach the cortex around the bottom of the superior temporal sulcus (*St₁*) or any other portion of the temporal cortex. Central sulcus (*C*), precentral (*CA*) and postcentral convolution (*CP*), inferior parietal convolution (*PI*), elevation of the cortex in the posterior portion of the Sylvian fossa comparable to the transverse temporal convolution of Heschl (*Ttr*), middle temporal convolution (*T₂*).

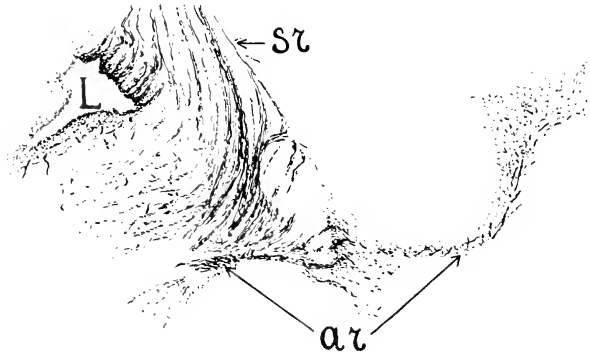


Fig. 31, Experiment I. A portion of a section close to that corresponding with the figure 30 under higher magnification. Somatic sensory radiation (*sr*) and the auditory radiation (*ar*) as in the preceding figure. The exact relation of the first to the latter is well demonstrated. External geniculate body (*Cgl*), Sylvian fossa (*FS*), thalamus (*Th*), superior (*T₁*) and middle temporal convolution (*T₂*).



Fig. 32, Experiment I. A portion of a section closely behind the level of the preceding figure under higher magnification (about 60 \times), showing the intimate relationship of the ventral thalamo-cortical and auditory fibers in the internal capsule (*Ci*). Dorsal brim of the external geniculate body (*Cgl*), claustrum (*Cl*), a portion of the cortex lining the Sylvian fossa (*FS*), putamen divided into larger and smaller islets (*Put*) by the fascicles of the auditory and ventral thalamic fibers, both entering the external capsule.

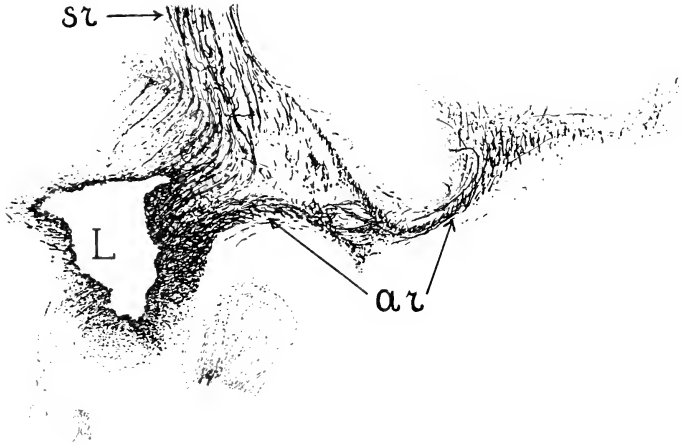


Fig. 33, Experiment I. A portion of a section just in front of the level of the figure 34, under higher magnification. Extensive lesion (*L*) of the posterior thalamus and of the internal geniculate body (*Cgm*) wherefrom numerous thalamo-cortical (*sr*) and the auditory fibers (*ar*) emerge. The auditory radiation is visible here in its entire length up to its termination in the ventral lip of the Sylvian fissure (*FS*). The level of this figure corresponds with the level immediately behind the posterior extremity of the lentiform nucleus. External geniculate body (*Cgl*), superior (*T₁*) and the middle temporal convolution (*T₂*).

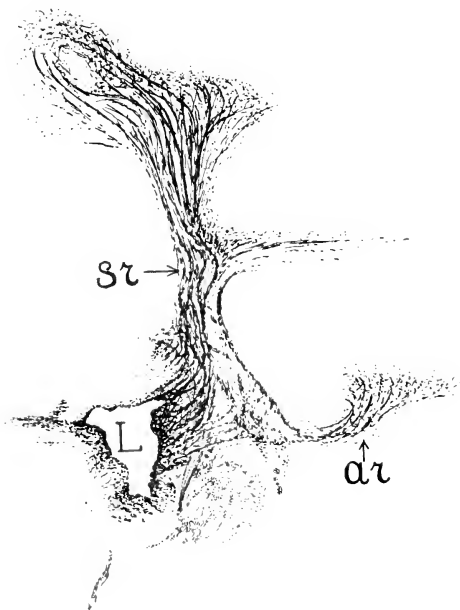


Fig. 34, Experiment I. A section showing the large lesion (*L*) in the posterior segment of the thalamus and pulvinar (*Pulv*), and in the internal geniculate body (*Cgm*). The posterior fan of the somatic sensory radiation (*sr*), composed of numerous fibers, enters the posterior limb of the internal capsule and takes a fairly direct ascending course toward the postcentral convolution (*CP*). Some fibers reach also the cortex lining the postcentral-intraparietal sulcus but none deviates toward the corpus callosum. A portion of the internal segment of the external geniculate body (*Cgl*) has also been injured. All auditory fibers enter the inferior lip of the Sylvian fissure (*FS*) belonging to the superior temporal convolution (*T₁*), none of them reaching the middle (*T₂*) or the inferior temporal convolution (*T₃*).

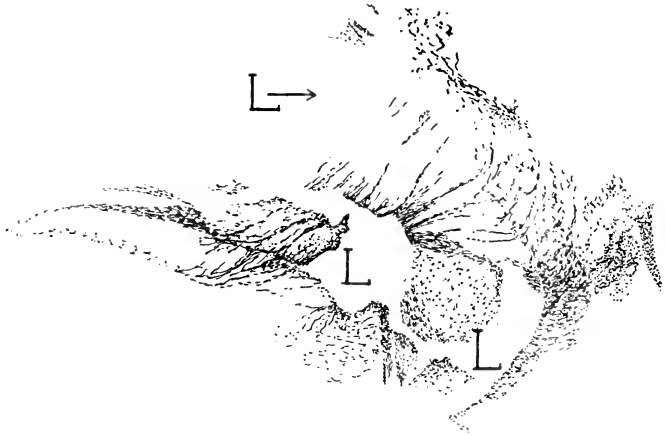


Fig. 35, Experiment I. This figure represents a portion of a section through the pulvinar (*Pulv*), through the anterior segment of the superior colliculus of the midbrain (*Colsup*), through the internal geniculate body (*Cgm*) and through the posterior spur of the external geniculate body (*Cgt*). The figure also shows the exact position and size of the multiple injuries (*L*) close to the spot where the knife penetrated into the betweenbrain from behind. (Compare with figs. 36, 37, 38.)



Fig. 36, Experiment I. A figure showing the section where the instrument reached the pulvinar from the internal capsule (*L* = lesions). All fiber bundles in the ventral portion of the pulvinar were interrupted and degenerated towards the superior colliculus of the midbrain (*Colsup*). They form the brachium of the colliculus and enter mainly the superficial medullary layer of the colliculus. (Compare with fig. 96.) The pulvinar is completely separated from the hemisphere. Superior parietal gyrus (*PS*), inferior parietal gyrus (*PI*).

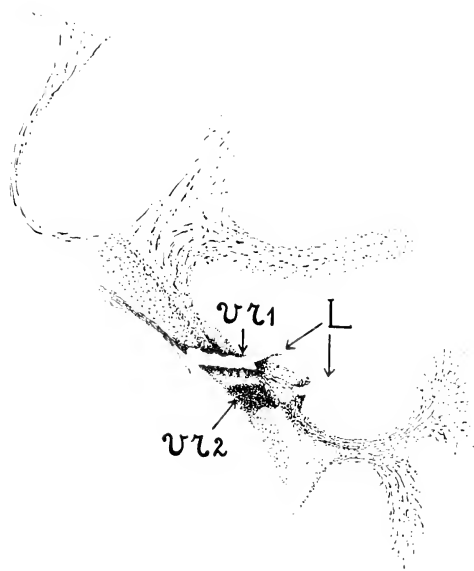


Fig. 37, Experiment I. A section behind the splenium of the corpus callosum, showing two narrow channels (*L*) which were produced by the instrument penetrating from behind and from the lateral side. (Compare with figs. 1 and 38.) These two small injuries interrupted two bundles of the sagittal fiber layers of the parieto-occipital lobes (*vr*₁ and *vr*₂) which are visible in the subsequent figures as separate degenerated bundles (figs 38, 39, 40, 41). Sylvian fissure (*FS*), inferior parietal gyrus (*PI*), superior parietal gyrus (*PS*), tapetum (*Tap*), superior temporal convolution (*T*₁), posterior horn of the lateral ventricle (*VL*).

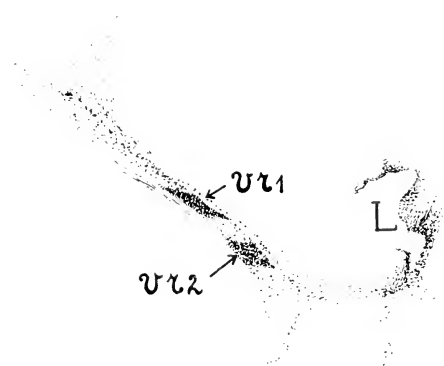


Fig. 38, Experiment I. Lesion (*L*) close to the surface of the hemisphere. Two degenerated segments of the external sagittal layer (*vr*₁ and *vr*₂) occupy about the intermediate portion of the sagittal fiber formation. Posterior extremity of the Sylvian fissure (*FS*), oral beginning of the calcarine fissure (*Fc*), inferior parietal gyrus (*PI*), superior parietal gyrus (*PS*), tapetum (*Tap*).



Fig. 39, Experiment I. This figure well demonstrates the shape and the position of the two degenerated segments (vr_1 and vr_2) of the external sagittal fiber layer of the parietal lobe, that is, of the visual radiation. Both degenerated zones occupy the perpendicular or vertical branch of the crescent-shaped external sagittal layer ($vert$), its superior (rhs) and inferior horizontal branches (rhi) containing only a few scattered degenerated fibers. None of the afferent degenerated visual fibers deviates as yet toward the striate cortex though the calcarine fissure (Fc) is fully developed (dotted intracortical stripe in the latter indicates the striate cortex); and none of the visual fibers turns toward the cortex covering the lateral face of the hemisphere. Angular gyrus (GA), inferior parietal gyrus (PI), superior parietal gyrus (PS).

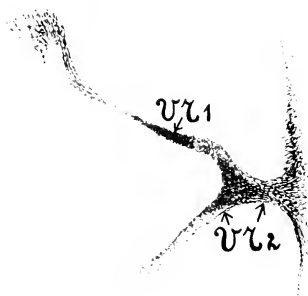


Fig. 40, Experiment I. In this figure the striate cortex (marked by an intracortical stripe) covering the occipital operculum (*Oo*) and close to its boundary along the simian fissure (*Ss*) appears. (Compare with fig. 1.) It is the ventral degenerated bundle (v_2) which enters this portion of the visual projection cortex. The dorsal degenerated bundle (v_1) proceeds further caudalward. Scattered degenerated fibers in both horizontal branches, notably in the upper branch, gradually deviate medially toward the lips of the calcarine fissure (*Fc*).

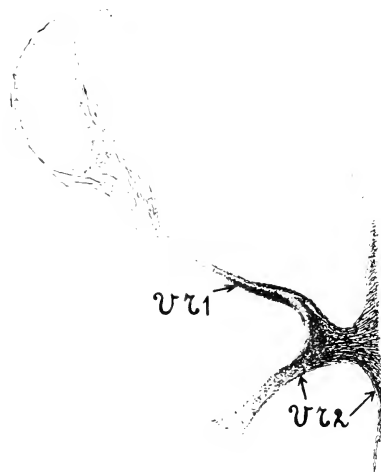


Fig. 41, Experiment I. The details in this figure are the same as in the preceding figure except that in the upper portion of the occipital operculum near the dorsal edge of the occipital lobe the striate cortex appears. To this go the scattered degenerated visual fibers from the upper horizontal branch of the visual radiation as well as the dorsal degenerated bundle (v_{11}). Calcarine fissure (Fc).



Fig. 42, Experiment I. This figure shows the striate cortex (marked by a dotted intracortical stripe) extending over the whole lateral face of the occipital lobe below and above the external calcarine sulcus, sulcus occipitalis superior (*Sos*). Here the upper degenerated bundle of the visual radiation of the preceding figure (*vr₁*) enters the cortex above the sulcus calcarinus externus (*Sos*) and the cortex lining the ascending branch of the calcarine fissure (*Fc*). (Compare with fig. 1.)



Fig. 43, Experiment I. A section close to the pole of the occipital lobe showing the striate cortex enveloping almost the entire lobe and supplied everywhere, especially on its lateral face, with degenerated afferent visual fibers. Posterior extremity of the calcarine fissure (*Fc*).



Fig. 44, Experiment II. Most anterior section of Experiment II, through the frontal lobe showing the superficial lesion (*L*) wherefrom a great number of fine callosal, association, and cortico-caudate fibers spring. The latter enter the subcallosal and zonal stratum of the caudate nucleus (*Nc*). Superior frontal convolution (*F₁*). (Compare with fig. 2.)

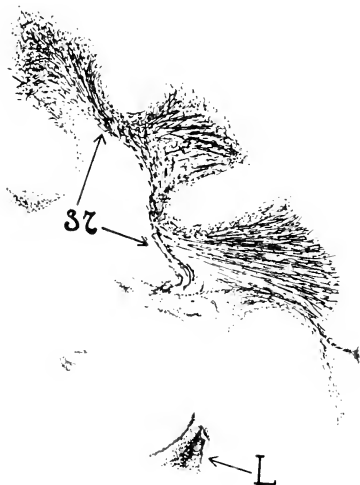


Fig. 45, Experiment II. The split-shaped lesion (*L*) reaches the extreme capsule and the claustrum. A fine bundle of corticofugal fibers springs from a small accidentally made lesion. A considerable number of afferent somatosensory fibers (*sr*), the anterior "fan" of the thalamo-cortical radiation, its origin visible in the following figures, reaches the precentral convolution (*Ca*) in its entire dorso-ventral extent. Caudate nucleus (*Nc*), putamen (*Put*).

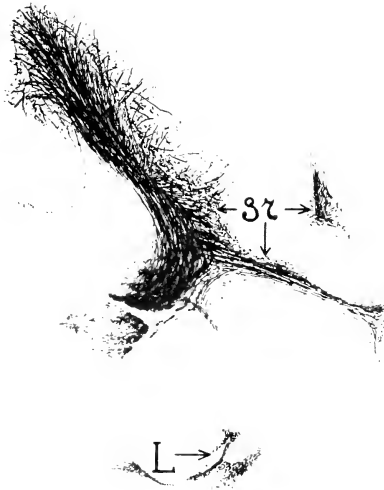


Fig. 46, Experiment II. The lesion (*L*) reaches the ventral portion of the putamen (*Put*) after penetrating through the external capsule and interrupting a bundle of fibers of the anterior commissure. First appearance of the central sulcus (*C*; its lower extremity; compare with fig. 2.) The middle "fan" of the thalamo-cortical radiation (*sr*) fully developed enters the cortex lining the central sulcus as well as that of both the precentral (*CA*) and of the postcentral convolution (*CP*) and the frontal operculum (*OF*). Sylvian fossa (*FS*), globus pallidus (*Gp*), caudate nucleus (*Nc*), superior temporal convolution (*T₁*).

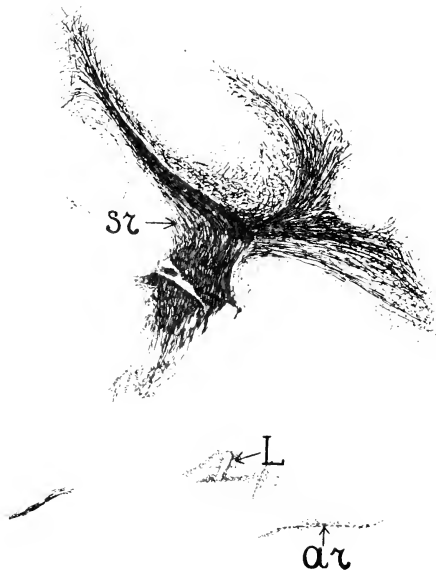


Fig. 47, Experiment II. The lesion (*L*) still within the putamen (*Put*) close to the anterior commissure and approaching the globus pallidus (*Gp*). The first appearance of the thalamus (*Th*), represented by its rostral segment remaining uninjured. Somatic sensory thalamo-cortical radiation (*sr*) as in the preceding figure except that its course toward the postcentral convolution (*CP*) is well demonstrated. Most of the degenerated fibers enter the cortex lining the floor of the central sulcus (*C*), not a small number reaching the precentral convolution (*CA*). Most rostral fibers of the auditory radiation (*ar*) close along the ventral spur of the claustrum enter the superior temporal convolution (*T₁*). Sylvian fossa (*FS*).

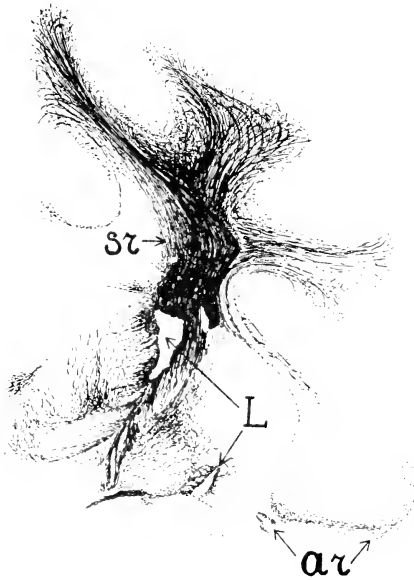


Fig. 48, Experiment II. Lesion (*L*) attains both the globus pallidus and the internal capsule. At the latter place, below the lesion, descending fibers; above it the thalamo-cortical radiation (*sr*) mainly tending toward the central sulcus (*C*) although both precentral (*CA*) and the postcentral gyri (*CP*) receive a considerable number of afferent fibers. Few of these reach the inferior parietal convolution (*PI*). Auditory radiation (*ar*) containing more fibers although not yet fully developed. It enters the upper lip of the superior temporal convolution (*T₁*) none of its fibers reaching any other portion of the temporal cortex. The position of the auditory fascicles within the sagittal fiber layer of the temporal lobe is well demonstrated. Many fibers degenerated in the thalamus (*Th*), the ascending belonging to lower afferent somatic sensory tracts. Sylvian fossa (*FS*), optic tract (*II*).

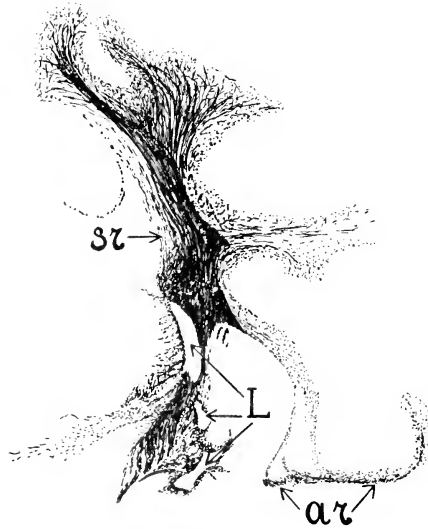


Fig. 49, Experiment II. Multiple lesions (*L*) in the globus pallidus and in the internal capsule, practically separating the thalamus (*Th*) from the hemisphere. The number of fibers of the thalamo-cortical radiation (*sr*) though still considerable is less than in the preceding figures. The main flow of the somatic sensory fibers is toward the central sulcus (the vestige of its cortex is visible in the upper corner of the figure as a small oval area). Some thalamic fibers enter the cortex around the intraparietal sulcus. Note that no fibers deviate toward the corpus callosum. (Compare with preceding and following figures.) The auditory radiation (*ar*) as before enters the upper lip of the superior temporal convolution (*T*), which forms the floor of the Sylvian fossa (*FS*). Optic tract (*II*) is slightly injured; inferior parietal convolution (*PI*); postcentral convolution (*CP*).

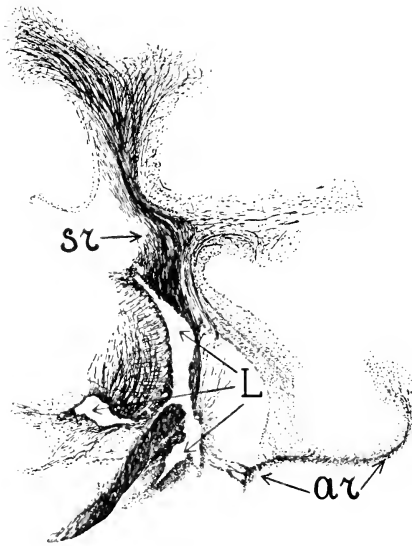


Fig. 50, Experiment II. The lesion (*L*), most extensive in this series, occupies almost the entire internal capsule besides destroying the globus pallidus and a portion of the optic tract (*II*), and penetrates into the ventral portion of the thalamus (*Th*) and into the hypothalamus. Within the lateral nucleus of the thalamus many degenerated ascending fiber bundles are visible (terminal branches of the median fillet and so forth). The thalamo-cortical radiation (*sr*), forming in reality a thick fiber sheet, ascends toward the superior parietal convolution (*PS*), which is the caudal continuation of the postcentral gyrus. Few degenerated fibers are visible in the cingulum, others in the inferior parietal convolution (*PI*). The auditory radiation (*ar*) is here already rich in fibers, all of them entering the upper lip of the superior temporal convolution (*T₁*), especially into an elevation of the cortex in the Sylvian fossa (*FS*) which might be compared with the transverse temporal convolution of Heschl in the human brain (*Ttr*). Some thin bundles ascend from the region of the putamen and enter the cortex around the dorsal corner of the Sylvian fossa.

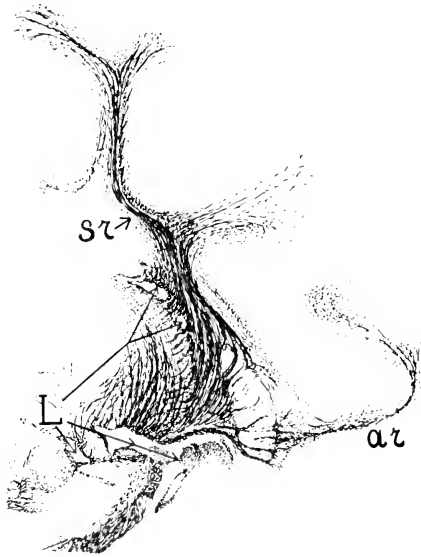


Fig. 51, Experiment II. The lesion (*L*) is reduced here to a series of small foci in the internal capsule and to two larger destructions of the hypothalamus. Of the external geniculate body (*Cgl*) the internal segment is destroyed without visible alteration of its middle and external segments. In the thalamus (*Th*) strong bundles of the incoming fillet are degenerated; their courses are chiefly parallel to one another and to the outer contour of the thalamus. Somatic sensory radiation (*sr*) reduced in size shows the characteristic appearance of a pine tree; it enters the superior parietal convolution (*PS*), some of its fibers forming the cingulum, others especially its ventral bundles along the putamen and through the latter nucleus reach the upper corner of the Sylvian fossa (*PS*) where the transverse temporal gyrus (*Ttr*) merges with the rest of the insular cortex. The auditory radiation (*ar*) visible immediately above the external geniculate body, penetrates through the ventral putamen and into the superior temporal convolution (*T_s*) where its fibers enter mainly the auditory "nuclear zone" in the transverse gyrus (*Ttr*).

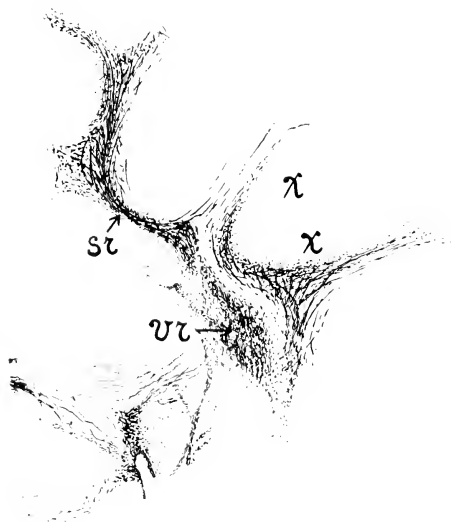


Fig. 52, Experiment II. Lesion reduced to a small injury of the internal geniculate body (*Cgm*), while the external geniculate body (*Cgl*) and the thalamus (*Th*) remain undamaged. In the white substance of the hemisphere three systems of degenerated fibers are visible: somatic sensory radiation (*sr*) tending toward the superior parietal convolution (*PS*), showing the mode in which a part of its fibers form the cingulum; the visual fibers (*vτ*) springing from the damaged internal segment of the external geniculate body (preceding figure), here somewhat scattered; and the fiber bundle supplying the cortex around the Sylvian fissure (*x, x*) which ascends from the ventral portion of the internal capsule (preceding figure). Inferior parietal convolution (*PI*), superior temporal convolution (*T₁*).

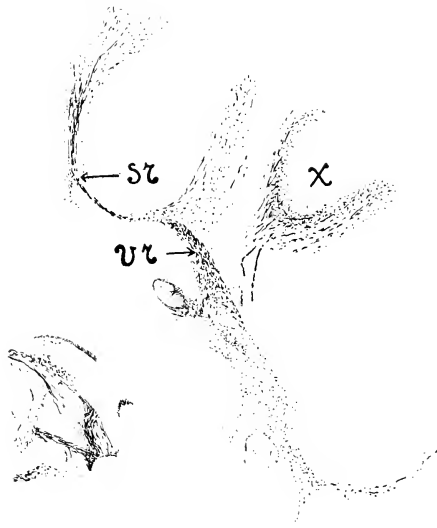


Fig. 53, Experiment II. Somatic sensory radiation (*sr*) in the posterior portion of the superior parietal convolution, much reduced in size. Visual radiation (*vr*) condensed already into the sagittal fiber layer of the parietal lobe and occupying the dorsal third of that fiber formation. The afferent fibers supplying the cortex around the posterior extremity of the Sylvian fissure (*x*) decreased in number. Inferior parietal convolution (*PI*), superior temporal convolution (*T₁*).

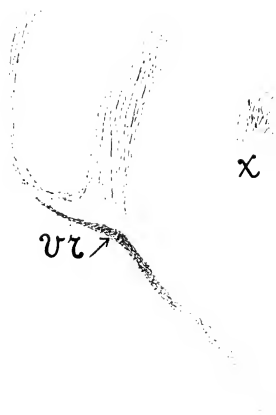


Fig. 54, Experiment II. Somatic sensory fibers in small number in the superior and inferior parietal convolution (*PS* and *PI*); degenerated portion of the external sagittal layer (visual radiation *vr*) forming a more compact zone than in the preceding figures; last afferent fibers to the posterior Sylvian region (χ); angular convolution (*GA*).

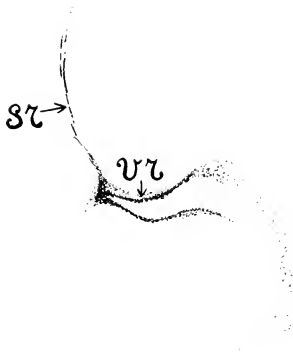


Fig. 55, Experiment II. Last somatic sensory fibers (*sr*) in the superior parietal convolution (*PS*); visual radiation (external sagittal stratum of the parieto-occipital lobe) taking here the shape of a horse-shoe facing medialward and embracing in its concavity the internal sagittal stratum, the tapetum, the lateral ventricle and the calcarine fissure (*Fe*). The visual radiation can be subdivided into a dorsal horizontal branch (*vr*, degenerated in this experiment), a ventral horizontal branch (*rhi*), and into a vertical or perpendicular branch (*rvert*) connecting both horizontal branches. Both the vertical and the ventral horizontal branches contain only a few scattered degenerated fibers. The visual afferent fibers of the degenerated dorsal horizontal branch (*vr*) bend in their ascending course occipitalward around the dorsal corner of the lateral ventricle and the tapetum and descend into the upper lip of the calcarine fissure where they reach the striate cortex (marked with a dotted stripe) first appearing in this series. None of the visual fibers deviates toward the non-striate cortex of the hemisphere. They go to a narrow strip of the area striata exclusively. Angular convolution (*GA*), simian sulcus (*SS*).



Fig. 56, Experiment II. The greater part of the fibers of the degenerated dorsal horizontal branch of the visual radiation (*vr*) has already descended into the upper lip of the calcarine fissure and forms here the dorsal half of the calcar avis. The degenerated visual fibers seen here supply a considerably more extensive portion of the striate cortex (marked with a dotted line) which approaches the brim of the upper lip of the calcarine fissure. The limit of the supplied cortex and of the striate cortex coincide exactly at the left side; on the right side the degenerated fibers stop at the bottom of the calcarine fissure. Although in this section the striate cortex extends over the entire lateral face of the occipital lobe (*Oo* = occipital operculum, compare with fig. 2) none of the degenerated afferent visual fibers enters it.

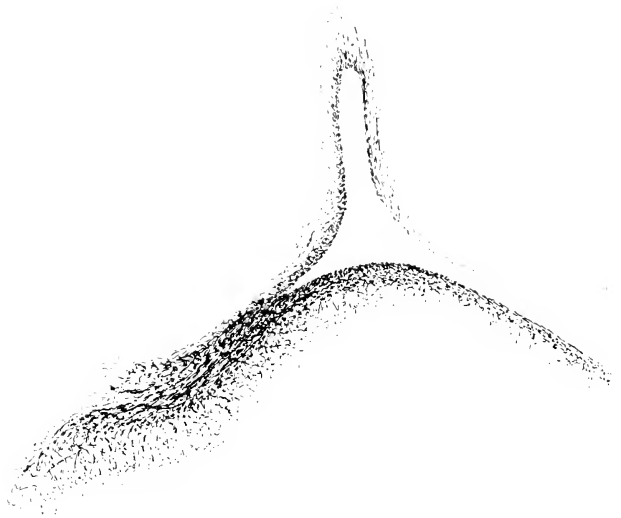


Fig. 57, Experiment II. A portion of the preceding figure under higher magnification showing the upper lip of the calcarine fissure. It shows the degenerated afferent visual fibers, black lines and dots, entering the striate cortex marked with number 17 and containing a dotted intracortical stripe. The first thing to be noted is that the visual fibers when still in the white substance keep close to the striate cortex, leaving other portions of that substance close to the nonstriate cortex (marked with number 18) entirely free. The exact coincidence of the boundaries of the cortex reached by degenerated fibers and of the striate cortex marked by an arrow (in the left side of the figure) is well demonstrated. None of the afferent visual fibers reaches the non-striate cortex. In this experiment a "boundary bundle," the most dorsal of the visual radiation originating in the internal segment of the external geniculate body (fig. 51) and forming the dorsal horizontal branch of the radiation, degenerated supplying the most dorsal strip of the entire striate area, the latter imagined stretched in a sagittal perpendicular plane. (Compare with figs. 2, 22, and 23.) This figure shows also the mode of turning of the external sagittal stratum around the dorsal edge of the tapetum.



Fig. 58, Experiment II. This figure as well as figures 59-61, and 62 shows under higher magnification (about 60 \times) the finer relations of the afferent thalamic fibers within the somatic-sensory cortex. Figure 58 corresponds with the anterior margin of the postcentral convolution or, what is the same, with the posterior lip of the central sulcus. (Compare with fig. 9.) Some degenerated fibers have an almost horizontal course within the lower cortical layers; others ascend obliquely toward the stripes of Baillarger, a portion of which is seen in the upper part of the figure. Note that only a few of the afferent fibers correspond to the actual "radiated" fibers (brown vertical fascicles remaining normal). Compare the number of afferent fibers with that in figures 60-62.

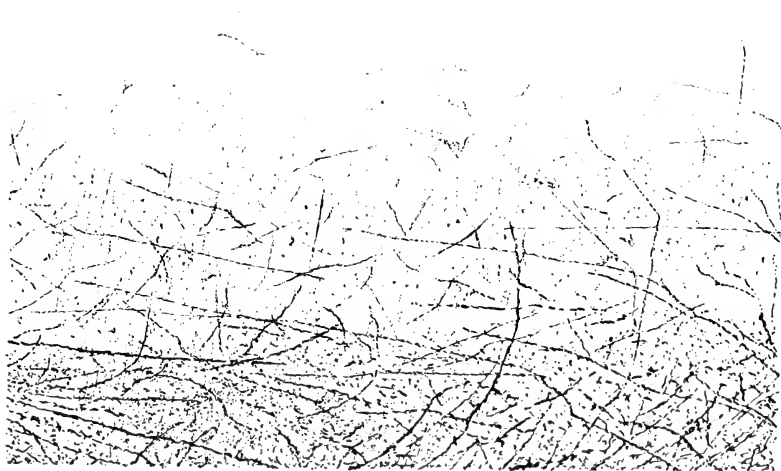


Fig. 59, Experiment II. This figure corresponds to the convexity of the postcentral convolution. It shows the finer relations of the afferent thalamic fibers to the postcentral granular cortex (fields 1 and 2 of Brodmann).

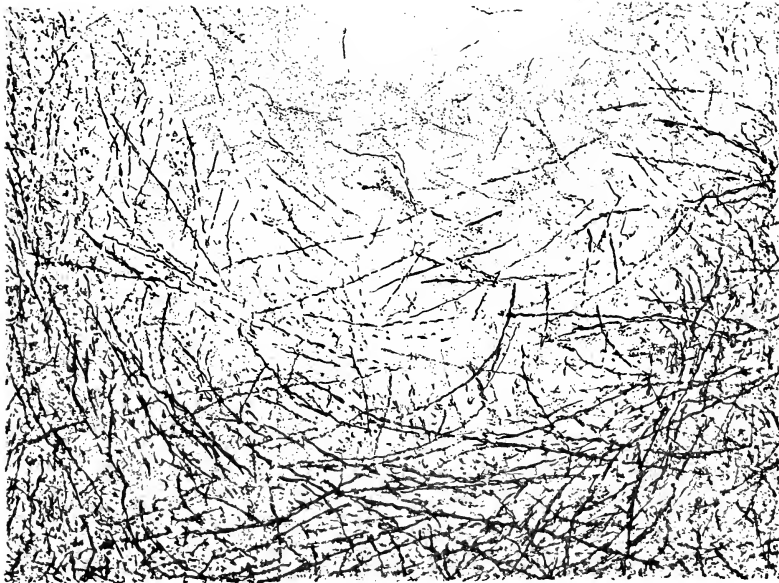


Fig. 60, Experiment II. This figure shows a portion of figures 9 and 48 corresponding with the bottom of the central sulcus, under higher magnification (about 60 \times). It shows the minute relations of the afferent thalamic fibers to that portion of the somatic sensory cortex which represents its "nuclear or focal zone." (Compare also with fig. 2 and 7.) This zone corresponds approximately with Brodmann's field 3 being the most anterior portion of the post-central granular cortex buried entirely in the central sulcus. This portion of the extensive pre-postcentral somato-sensory region is most richly supplied by the afferent fibers originating in the thalamus. The number of exogenous fibers in the infragranular cortical strata is here considerably above that either in the agranular precentral "motor" cortex or field 4 of Brodmann (figs. 61, 62), or in the remaining postcentral granular cortex or fields 1 and 2 of Brodmann (figs. 58, 59). The stripes of Baillarger, the semicircular finely dotted zone in the upper portion of the figure, is filled with the fine black detritus of the disintegrated myelin. A few fine degenerated fibers, however, reach the supra-granular layers as shown also in figure 9.

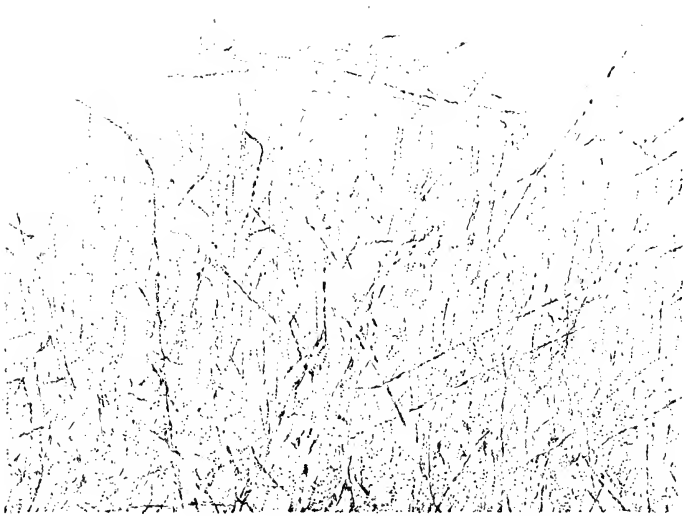


Fig. 61, Experiment II. This figure shows finer details of the afferent exogenous fibers in the precentral agranular "motor" cortex, area gigantopyramidalis or field 4 of Brodmann. (Compare with figs. 6 and 7.) Although here a number of exogenous fibers approach the course of the "radiated" fibers, many show a more or less oblique direction being distinct from the actual radiary bundles. (Compare with figs. 63, 64.) Some especially close to the and within the stripes of Baillarger (upper part of the figure) have even an horizontal course. The number of exogenous fibers in the "motor" cortex appears to be rather greater than in the postcentral areas 1 and 2, as comparison of this figure with figures 58 and 59 demonstrates; it is, however, below that of the "focal zone" of the somatic sensory cortex. (See preceding figure.)

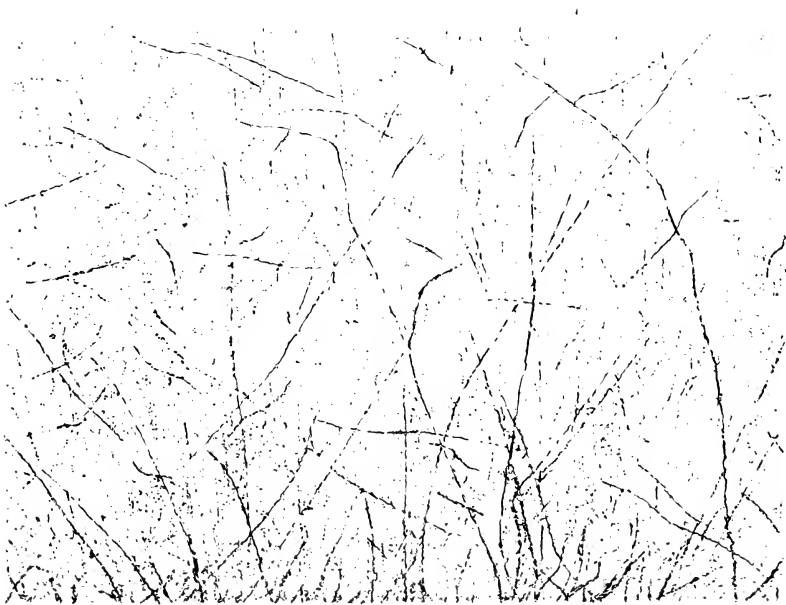


Fig. 62, Experiment II. This figure taken from the convexity of the precentral convolution shows, as does figure 61, the finer relation of the afferent fibers to the agranular precentral "motor" cortex. The course of many exogenous fibers, distinct from that of the actual "radiated" fibers, is here more accentuated than in the preceding figure. (Compare with figs. 63 and 64.)

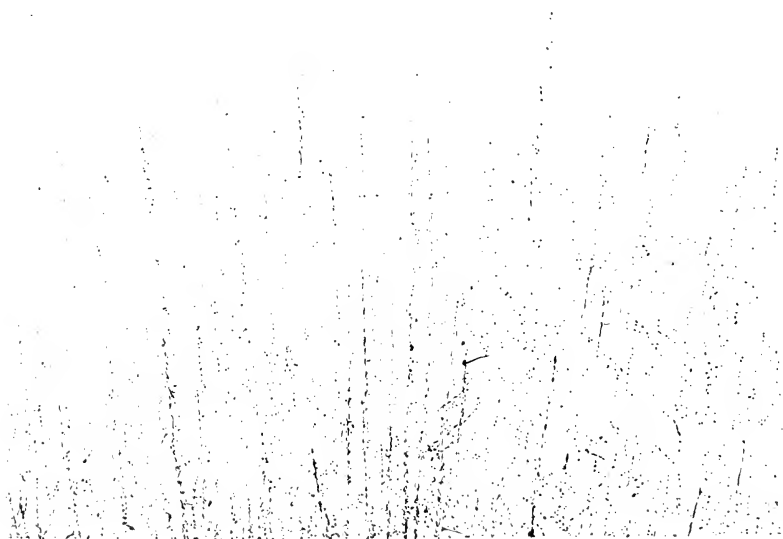


Fig. 63, Experiment VI. This figure shows under the same magnification as figures 58-61, and 62, finer relations of the incoming association fibers in the precentral "motor" cortex originating from the postcentral granular cortex (that is, from a convexity of the middle third of the postcentral convolution). All degenerated fibers exhibit a course identical with that of the "radiated" bundles and distinct from that of the exogenous thalamic fibers of the same region (figs. 61, 62).

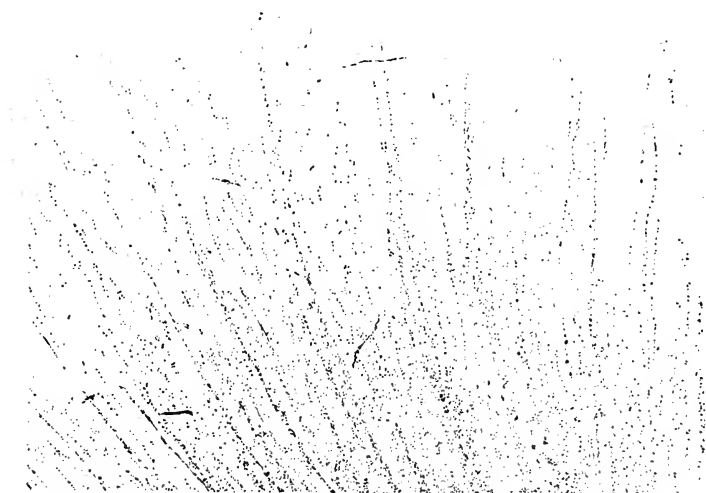


Fig. 64, Experiment VI. This figure shows the same details as the preceding figure. It corresponds to the convexity of the upper third of the precentral convolution.



Fig. 65, Experiment II. This figure represents the upper lip of the calcarine fissure of figure 56 at a higher magnification (about $50\times$) and turned upside down, showing finer relations of the afferent visual fibers to the striate cortex. Field 17 or striate area (marked by number 17) contains three intracortical layers characteristic of the striate cortex, the uppermost of these corresponding with the stria Gennari-Vieq d'Azyr. The limit of the striate cortex at the right extremity of the figure marked by an arrow. In the cortex itself many degenerated afferent visual fibers do not quite correspond to the "radiated" bundles, some of the first observing a more or less horizontal or oblique course within the lower layers. As the afferent visual fibers reach the stripe of Gennari or Vieq d'Azyr they become thinner and sparser. Note the gradual decrease in thickness of the three intracortical stripes toward the boundary of the striate cortex.

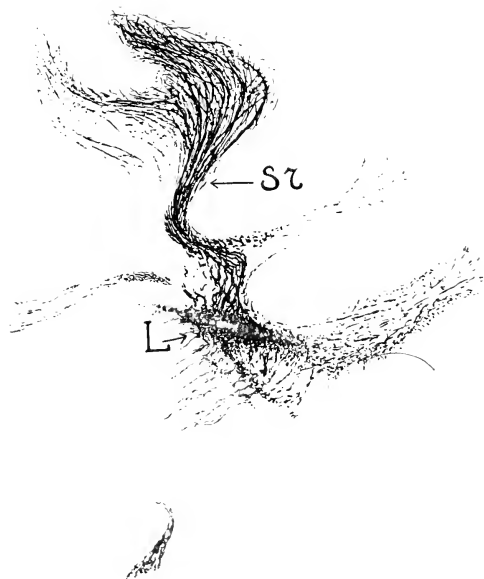


Fig. 66, Experiment III. This figure shows the most anterior section of the series with the lesion (*L*) in the posterior limb of the internal capsule, interrupting the posterior "fan" of the thalamocortical radiation (*sr*). The latter reaches the cortex around the upper extremity of the central sulcus, most of its fibers, however, entering the post central convolution (*CP*). Precentral convolution (*CA*), inferior parietal convolution (*PI*), thalamus (*Th*). (Compare with fig. 3.)

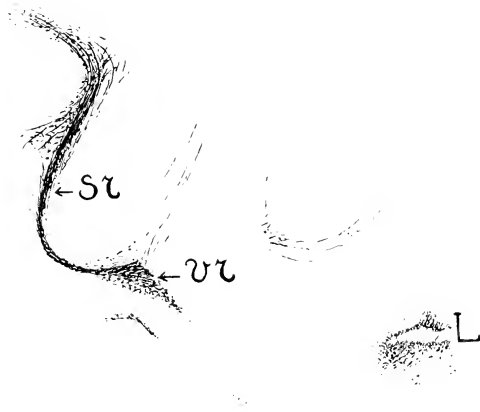


Fig. 67, Experiment III. Superficial lesion (*L*) through which the instrument entered the substance of the hemisphere. (Compare with fig. 3.) Somato-sensory radiation (*sr*) entering the superior parietal convolution (*PS*), the visual radiation in as much as it was interrupted forms a degenerated zone in the upper portion of the external sagittal stratum of the parietal lobe (*vr*). Inferior parietal convolution (*PI*) with the Sylvian fissure, the latter receiving a few afferent fibers. (Compare with *x* in figs. 52-54.) A bundle of callosal fibers in the tapetum, and a bundle of the efferent fibers in the internal sagittal stratum degenerated.

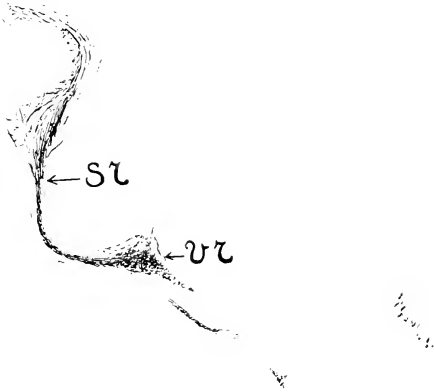


Fig. 68, Experiment III. Somato-sensory afferent fibers (*sr*) still in connection with the common degenerated zone of the external sagittal stratum containing degenerated visual fibers (*vr*). A bundle of callosal fibers in the tapetum and a bundle of efferent fibers in the internal sagittal stratum degenerated. Inferior parietal (*PI*) and superior parietal convolution (*PS*).

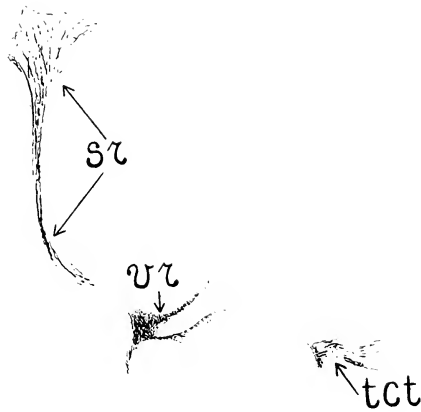


Fig. 69, Experiment III. A figure corresponding with the level behind the splenium of the corpus callosum showing the beginning of the calcarine fissure and the well formed crescent shaped visual radiation; its dorsal horizontal branch degenerated (*vr*), the visual fibers bending around the tapetum into the upper lip of the calcarine fissure where they enter the striate cortex still occupying only a portion of that fissure. Somato-sensory fibers (*sr*), definitely separated from the visual, enter the superior parietal convolution (*PS*). A few degenerated cortico-fugal fibers pass between the bundles of the external sagittal stratum to reach the internal sagittal stratum (*tct* = tractus cortico-tectalis). (Compare with figs. 95, 96.)

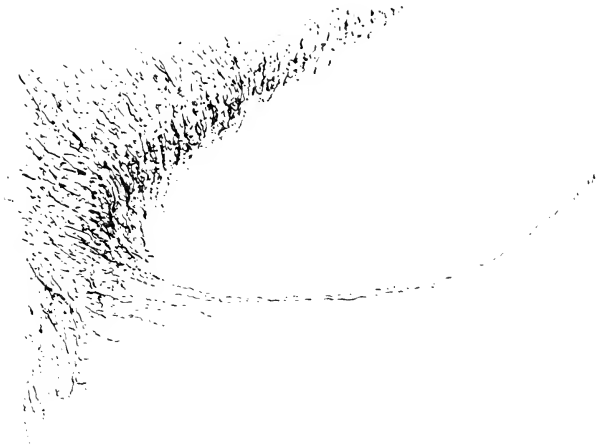


Fig. 70, Experiment III. A portion of figure 69 under higher magnification showing the quite gradual bending of the dorsal horizontal branch of the visual radiation (*Ssl* = stratum sagittale laterale) around the internal sagittal stratum (*Ssm*) and the tapetum (*Tap*) to reach the upper lip of the calcarine fissure. The visual fibers do not reach the striate cortex (marked with *I7*) here but farther occipitalward (fig. 71) though a few fibers enter already here the calcar avis. Parastriate cortex (*I8*).

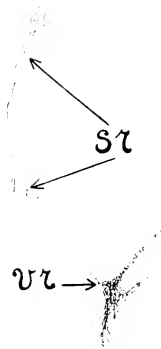


Fig. 71, Experiment III. Last somato-sensory fibers (*sr*) in the superior parietal convolution (*PS*). Fibers of the upper horizontal branch of the visual radiation (*vr*) already in great part in the upper lip of the calcarine fissure where they enter the here more extensive striate cortex (marked by a dotted intracortical stripe). None of the degenerated afferent visual fibers enters any other portion of the occipital-parietal cortex or even of the striate cortex. Angular convolution (*GA*.)



Fig. 72, Experiment III. The upper lip of the calcarine fissure of figure 71 under higher magnification. It shows the upper horizontal branch of the visual radiation degenerated and already descended into the upper lip. (Compare with fig. 57.) The visual fibers supply exclusively the striate area marked with number 17, which contains a double dotted intracortical stripe, its boundary marked by an arrow. Since in this experiment the "boundary bundle" of the visual radiation was interrupted, the limit of the supplied cortical segment and of the striate cortex coincides exactly. None of the afferent visual fibers enters the non-striate cortex (marked with 18) or even approaches it.

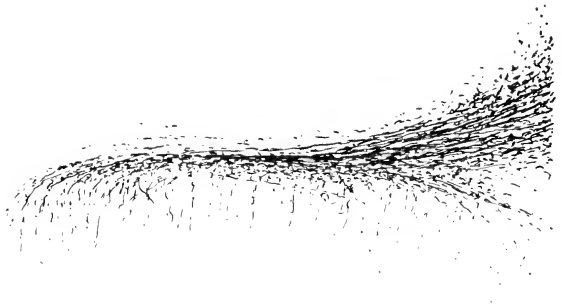


Fig. 73, Experiment III. A portion of the upper lip of the calcarine fissure of the preceding figure showing finer relations of the afferent visual fibers and the striate cortex. The afferent fibers cease abruptly at the point of cessation of the three intracortical stripes (marked by an arrow) characteristic of the striate cortex (17), none of these fibers reaching the parastriate cortex (18). Also that portion of the white substance nearer to the parastriate cortex remains free from any degenerated afferent fibers (in the upper portion of the figure).



Fig. 74, Experiment III. A section through the posterior portion of the occipital lobe showing the deep main branch and the ascending branch of the calcarine fissure (*Fc*) both lined by the striate cortex which also covers the lateral face of the lobe (occipital operculum = *Oo*). Degenerated afferent visual fibers enter exclusively a portion of the striate cortex marked by a dotted intracortical stripe in the upper lip of the main branch of the calcarine fissure (*lower Fc*), and that portion of the striate area which is in front of the ascending branch of the calcarine fissure (in this figure immediately below the upper *Fc*; compare with fig. 3).



Fig. 75, Experiment IV. In this experiment, to which figure 76 also belongs, a portion of the dorsal horizontal branch and in addition to it, the nearby portion of the vertical branch of the visual radiation were interrupted. In contrast to Experiments II and III (figs. 55-57, 69-73, and 74), where the dorsal rib of the radiation supplying the upper lip of the calcarine fissure degenerated alone and was interrupted completely, here the interruption of the upper horizontal branch was incomplete, its most internal bundle being left unaltered; yet the destruction extended to the nearby portion of the vertical branch. The degenerated bundle of the visual radiation is therefore somewhat different and supplies in oral planes corresponding with figure 75, only the lateral half of the striate cortex of the upper lip closer to the bottom of the fissure (zone *a-b*), leaving the actual "boundary zone" between the letter (*a*) and the arrow with normal fibers. In this experiment the interrupted bundle becomes a "boundary bundle" only in more caudal sections corresponding with figure 76, where its fibers spread as far medially as the striate cortex extends (boundary of the striate cortex containing a double intracortical stripe marked by an arrow). No afferent visual fibers whatever enter into the parastriate cortex marked with number 18. Furthermore this figure illustrates the manner in which the dorsal horizontal branch reaches the upper lip. Its fibers do not turn in one and the same plane medially, but only gradually by slowly ascending in their course occipitalward and slowly bending around the narrow ridge of the fiber fold formed by the tapetum, and again descending toward the upper lip where they turn again in part in the rostral direction. Thus the bundles before reaching the striate cortex describe a spiral, those destined for the oral segments of the upper lip forming at the same time an arc in the sagittal plane with its concavity turned rostrally; this arc, therefore, remains in figure 75 incomplete, being completed in caudal levels represented by figure 76. Note the sharp line of demarcation between the degenerated and normal segments of the external sagittal layer. Lower lip (*Li*), upper lip (*Ls*) of the fissura calcarina (*FC*).

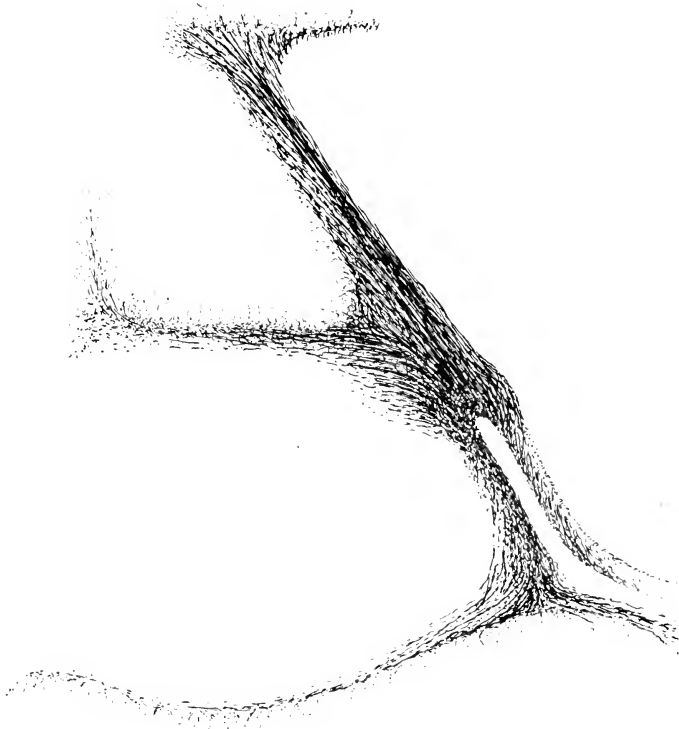


Fig. 76, Experiment IV. This figure represents a section caudal to the plane of figure 75. (Compare also fig. 74.) It shows the striate cortex, marked by number 17, coating the calcarine fissure (*FC*) and extending over the internal face of the occipital lobe (upper part of the figure, corresponding with the upper edge of the occipital lobe). Thus in the same section portions of the striate cortex (17) alternate with those of the area parastriata (18). The boundaries of the striate area (where the stria Gennari or Vieq d'Azyr, double dotted intracortical stripe, ceases), are marked by arrows. This figure demonstrates the fact that the afferent visual fibers reach the striate cortex exclusively. Note the manner in which visual fibers reach the upper lip of the calcarine fissure and partly enter the calcar avis (latter beginning in the right lower corner of the figure); the figure also demonstrates clearly the complete avoidance by afferent visual fibers of those portions of the medullary white substance which are closer to the non-striate cortex. (Compare fig. 12.)

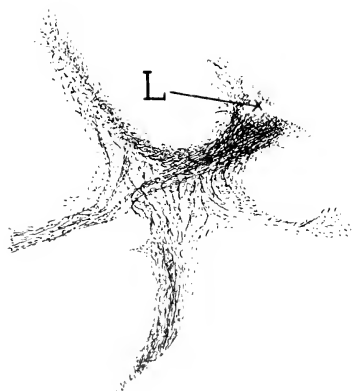


Fig. 77, Experiment VI. In this experiment as well as in Experiment V the convexity of the postcentral convolution (*CP*) was destroyed. The lesion (*L*) is confined either to the cortex alone or it extends for a short distance into the subjacent white substance (*1 mm.*). Besides numerous association and callosal fibers, a considerable number of fine, medium sized and a few coarse efferent fibers are degenerated; the latter descend into the internal capsule, as the figure shows, in the lateral half of the cerebral peduncle and farther caudward. None of the postcentral efferent fibers terminates in the peduncle, in the substantia nigra, in the red nucleus, or in the caudate nucleus, few only entering the globus pallidus. (Compare with Experiments VII, VIII, IX, figs. 78-85.) Precentral convolution (*CA*), Sylvian fossa (*FS*).



Fig. 78, Experiment VII. In this experiment the lesions (*L*) are confined to the precentral convolution (*CA*) all the rest of the hemisphere remaining unimpaired. Besides numerous association and callosal fibers many corticofugal fibers degenerated. They are: numerous fine fibers descending from Brodmann's field 6, numerous coarse fibers descending from Brodmann's field 4 (pyramidal fibers of the precentral "motor" area); numerous fine efferent fibers entering the caudate nucleus (*NC*) and the stratum subcallosum, numerous medium sized fibers reaching the upper corner of the globus pallidus (*Gp*), the number of the latter being hardly less than that of the pyramidal fibers; a considerable number of fairly coarse fibers reaches the stratum intermedium of the peduncle, the substantia nigra and the reticulate substance of the mid-brain, ventral tegmental field and dorsal pontine nuclei. (Compare Experiment VIII, figs. 80-84, and my paper, 1928.) None of the pyramidal fibers decussates in the corpus callosum to reach in this way the opposite peduncle. The pyramidal tract forms the middle third of the peduncle of the same side. Internal capsule (*Ci*), Sylvian fossa (*FS*), globus pallidus (*Gp*), putamen (*Put*).



Fig. 79, Experiment VII. This figure shows the same details as the preceding figure. Precentral convolution (*CA*), postcentral convolution (*CP*), Sylvian fossa (*FS*), globus pallidus (*Gp*), caudate nucleus (*Nc*), putamen (*Put*), thalamus (*Th*).

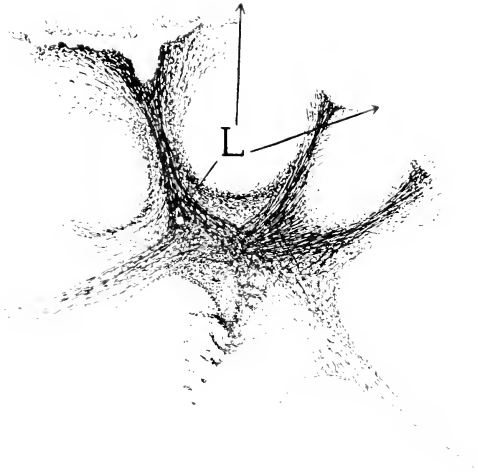


Fig. 80, Experiment VIII. In this experiment portions of the precentral and frontal cortex and a part of the subjacent white substance of the frontal lobe were destroyed. The lesion (*L*) remains confined to the cortex and to the nearby white substance with the exception of a single small lesion visible in this figure, the deepest in the series. Besides this, a small cortical injury of the post-central convolution opposite the precentral lesion in figure 81 was found. Beside numerous association and callosal fibers, the following efferent fibers degenerated: (1) very numerous and very fine fibers to the head of the caudate nucleus (*Nc*) and to its stratum zonale and str. subcallosum, (2) others of medium size forming the innermost segment of the cerebral peduncle to the stratum intermedium of the peduncle and to the substantia nigra, (3) others to the globus pallidus, and finally (4) the pyramidal fibers. No descending fibers from the precentral and from the convex frontal cortex (from field 4, 6, 8, 9 of Brodmann) enter the red nucleus or the roof of the midbrain. Superior frontal convolution (*F₁*). (Compare with fig. 7 and figs. 81-85, 96.)



Fig. 81, Experiment VIII. This figure shows bundles of degenerated precentral-frontal fibers entering the globus pallidus (*Gp*). Precentral convolution (*CA*), postcentral convolution (*CP*), lesion (*L*), caudate nucleus (*Ne*), putamen (*Put*). In the anterior limb of the internal capsule two separate degenerated zones corresponding to the two isolated injuries of the precentral motor area.

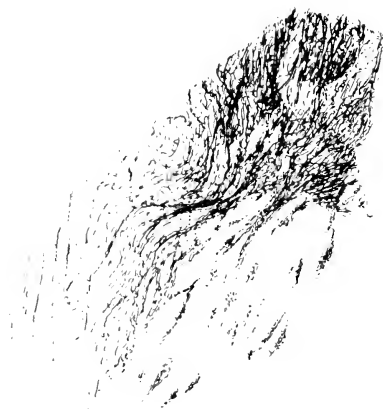


Fig. 82, Experiment VIII. This figure shows a portion of the preceding figure under higher magnification. Some of the degenerated bundles enter from the internal capsule (*ci*) into the upper salient of the globus pallidus (*Gp*). Putamen (*Put*).



Fig. 83, Experiment VIII. This figure shows degenerated corticofugal fibers of the frontal lobe entering the stratum intermedium of the peduncle (*Sip*) and the substantia nigra (*Sn*). External geniculate body (*Cgl*), subthalamic nucleus of Luys (*CL*), caudate nucleus (*Nc*), putamen (*Put*), thalamus (*Th*).



Fig. 84, Experiment VIII. A portion of the preceding figure under higher magnification. Descending fibers from the frontal lobe gradually enter the stratum intermedium of the peduncle (*Sip*) and the substantia nigra (*Sn*). Cerebral peduncle (*Pp*).

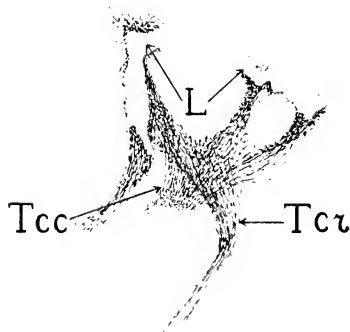


Fig. 85, Experiment IX. In this experiment fields 9, 10, 12, and probably also 32 of Brodmann in the frontal lobe (*LF*) were injured (*L*). In this figure representing a horizontal section through the hemisphere the course of the frontal cortico-caudate fibers (*Tcc*) and of the cortico-rubral fibers (*Tcr*) is visible. The first terminate in the stratum subcallosum, while the termination of the second in the red nucleus is not visible in this plane. Caudate nucleus (*Nc*), putamen (*Put*), and the internal capsule in between. (Compare fig. 7.)

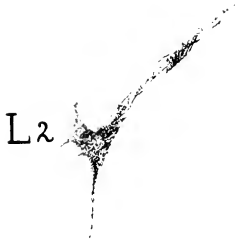


Fig. 86, Experiment XIV. This figure and the subsequent figures 87-94 represent sections through a hemisphere where two small injuries were produced in the occipital lobe (macular portion of the striate area; compare figs. 21 and 25). The injuries as figures 86 and 87 show are strictly limited to the cortical substance hardly reaching the subcortical fiber layers. From these injuries a great number of fine and a few coarser association fibers arise, which partly enter the surrounding striate cortex, partly the peri-parastriate area (fig. 25). Calcarine fissure (*Fe*), lower lesion (*L₂*).

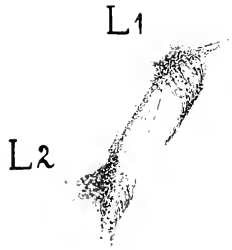


Fig. 87, Experiment XIV. Both upper (L_1) and lower cortical lesion (L_2) of the occipital operculum are visible, from each a great number of fine association fibers emerge. These keep either close to the cortex, or enter in well formed bundles the sagittal layers of the occipital lobe. Calcarine fissure (Fc).



Fig. 88, Experiment XIV. In this figure still numerous association fibers are visible in the white subcortical substance of the occipital operculum (*Oo*); others form two degenerated zones of the sagittal strata, notably of the external sagittal stratum. Stripe of Gennari-Vicq d'Azyr is not composed of association fibers of any considerable length. Calcarine fissure (*Fc*).



Fig. 89, Experiment XIV. A section close to the anterior boundary of the striate area covering the occipital operculum (*Oo*), and near to the simian sulcus (*Ss*; compare with figs. 21, 25). In the opercular white substance the number of degenerated fibers is decreasing; in the sagittal strata the number is approximately the same. Calcarine fissure (*Fc*).



Fig. 90, Experiment XIV. Within the opercular subcortical substance the number of degenerated fibers is still further decreased, this substance as well as the striate cortex of the occipital operculum (*Oo*) is divided into two halves by the forward thrust of the cortex of the simian sulcus (*Ss*). From the upper degenerated zone of the sagittal strata, numerous association fibers begin to ascend to reach here, and in the following sections, the cortex around the upper extremity of the simian sulcus. Calcarine fissure (*Fc*).



Fig. 91, Experiment XIV. The last vestige of the opercular subcortical substance contains a few degenerated fibers (close below *Oo*). Numerous degenerated fibers from the sagittal strata ascend and enter a well delimitable segment of the cortex in the upper portion of the simian sulcus (*Ss*) here fully developed. No such fibers reach the lower portion of that sulcus. Calcarine fissure (*Fc*), Occipital operculum (*Oo*).



Fig. 92, Experiment XIV. In this figure the cortical segment supplied by the upper degenerated bundle of the sagittal strata (in figs. 90, 91) now emerges on the free face of the hemisphere and is reduced in size. The remaining degenerated fibers of the sagittal strata begin to ascend toward the cortex and enter the upper portion of the angular convolution (*GA*). Calcarine fissure (*Fe*).



Fig. 93, Experiment XIV. This figure well demonstrates the degenerated association fibers from the visual projection cortex finally entering a circumscribed segment of the angular convolution (*GA*), or the area peri-parastriata of Elliot Smith (Brodmann's fields 18, 19). No other region of the parietal cortex receives these fibers in the present experiment. Superior parietal convolution (*PS*).



Fig. 94, Experiment XIV. Last degenerated association fibers from the striate area enter the cortex of the angular convolution (*GA*). Superior parietal convolution (*PS*). In figure 25 the shaded area in front of the simian sulcus represents only a portion of the peri-parastriate area which receives association fibers, other portion being buried within the simian sulcus. Within the cortex, the association fibers from "radiated" bundles. No other fibers (long association fibers, callosal and efferent fibers) were seen in the present experiment.

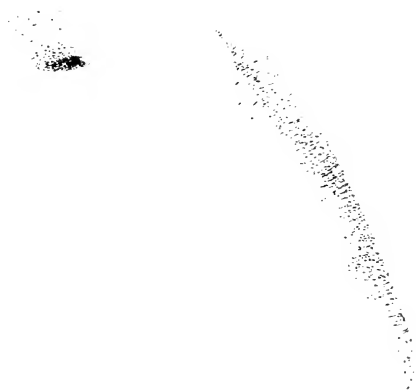


Fig. 95, Experiment XV. In this experiment the cortex around the dorsal extremity of the simian sulcus was damaged (Brodmann's fields 18, 19). From the lesion two distinctive fiber systems enter the sagittal layers of the parietal lobe: (1) a thin well circumscribed bundle in the tapetum (*Tap*) which enters exactly the same position in the tapetum, (2) another group of fibers which enter the splenium of the corpus callosum and occupies in the opposite hemisphere the external sagittal layer (*Ssl*) and to a slight extent the internal sagittal layer (*Ssm*) and finally pass through the pulvinar of the thalamus by forming the brachium of the superior colliculus to reach the roof of the midbrain. (Compare next figure.) In other experiments it was found that the internal sagittal layer is composed of efferent fibers. (Compare figs. 68, 69.)



Fig. 96, Experiment XV. This figure showing a section through the pulvinar (*Pulv*) and the superior colliculus of the midbrain (*Colsup*) demonstrates the mode in which the efferent fibers from the peri-parastriate area (Brodmann's fields 18, 19) reach the roof of the midbrain. Tractus cortico-tectalis (*Tct*).

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INDEX

- Accord (in audition), 99.
- Acuity of central (macular) vision, 178.
- Adaptation to environment, 223.
- Afferent auditory fibers. *See* Radiation.
- Afferent fibers. *See* Fibers; Radiation.
- Afferent pathways and cerebral cortex, 211.
- Afferent paths (perfection), 222, 225.
- Afferent paths (spatial organization), 41, 44, 70, 73, 94, 101, 104, 117, 124, 142, 158, 161, 187, 189, 191, 192, 193, 197, 205, 219.
- Afferent paths (structure and biological significance), 219-226.
- Afferent somato-sensory fibers. *See* Radiation.
- Afferent visual fibers. *See* Radiation.
- Aggregation. *See* Mosaic.
- Agnosia (visual), 136.
- Area peri-parastriata, 166, 213, 218.
- Area striata. *See* Cortex.
- Area striata (associational connections). *See* Fibers.
- Area striata (electrical stimulation), 175.
- Areas, associational (cerebral), 212, 214, 218.
- Areas, projectional (cerebral), 211, 212, 214.
- Areas, projectional, in monkey (scheme), 212.
- Arteria fissurae calcarinae, 181.
- Association areas. *See* Areas.
- Association fibers. *See* Fibers.
- Auditory cortex. *See* Cortex.
- Auditory path. *See* Radiation.
- Auditory radiation. *See* Radiation.
- Auditory system, 9, 79, 101.
- Auditory system (function). *See* Function.
- Basal meshwork. *See* Meshwork.
- Bilaterality of macular projection. *See* Macula; Unilaterality.
- Bilaterality of somato-sensory radiation. *See* Unilaterality.
- Biological significance of afferent paths, 219-226.
- Biological significance of central nervous system, 220.
- Blood supply of occipital lobe (pole), 181, 183, 205.
- Boundary bundles of visual radiation. *See* Radiation.
- Boundary zones of visual cortex. *See* Cortex.
- Brachium of superior colliculus, 71, 162, 240, 241, 301.
- Brain (organization, function). *See* Decentralistic concept; Continuum; Dynamists; Equipotentiality; Flechsig's concept; Localistic concept; Lashley's areal equipotentiality; Omnivalence.
- Calcar avis, 112, 122, 128.
- Calcarine fissure. *See* Fissura.
- Central nervous system (biological significance), 220.
- Central sulcus. *See* Sulcus.
- Central vision. *See* Macular vision.
- Cerebral cortex. *See* Brain; Cortex.
- Cochlea (cerebral projection), 86, 93, 104.
- Cochlea (function), 92-100.
- Cochlea (nervous supply). *See* Fibers, 93-98.
- Colliculus superior, 24, 25, 151, 162.
- Colliculus (brachium). *See* Brachium.
- Configuration doctrine. *See* Figures, Whole.
- Consonance (in audition), 97, 99, 100.
- Continuum (cerebral) of Gurwitsch, 196, 197.
- Convolution of Heschl. *See* Heschl.
- Corpus (griseum) praegeniculatum, 151, 162.

Index

- Cortex, auditory, 9, 81, 83, 87, 88, 89, 90, 91, 102, 103.
- Cortex, auditory (focal zone), 89, 103.
- Cortex, auditory (segmentation), 101.
- Cortex (basal meshwork), 156.
- Cortex, cerebral (general), 1.
- Cortex, cerebral (organization, function). *See* Brain; Function.
- Cortex, macular. *See* Macula, Macular, 127, 134, 135, 175, 176, 180.
- Cortex, macular (human), 176.
- Cortex, macular (association connections). *See* Fibers.
- Cortex, macular (function). *See* Function.
- Cortex, motor, 5, 66, 67, 68.
- Cortex, postcentral (function). *See* Function.
- Cortex, precentral (function). *See* Function.
- Cortex, sensory-motor, 66.
- Cortex, somato-sensory extent, boundary, 5, 47, 61, 74.
- Cortex, somato-sensory (function). *See* Function.
- Cortex, somato-sensory (nuclear or focal zone), 48, 55, 56, 61, 63, 69, 75, 263, 264, 265, 266, 267.
- Cortex, somato-sensory (segmentation), 64, 67, 68, 73.
- Cortex, visual (area striata), 12, 50, 107, 124, 157, 165, 166, 199, 200, 217, 262, 270, 278, 280, 281, 291-299.
- Cortex, visual (area striata), in man, 176.
- Cortex, visual (boundary zones, segments), 28, 33, 39, 43, 115, 116, 117, 121, 122, 124, 158, 171, 245, 246, 247, 248, 260, 261, 262, 270, 274, 277, 278, 279, 280, 281.
- Cortex, visual (comparative), 50, 197, 198.
- Cortex, visual (development), 128, 129.
- Cortex, visual (Gennari-Vieq d'Azyr's stripe), 153, 154, 155, 161, 196.
- Cortex, visual (segmentation), 158, 161, 188, 191.
- Cortex, visual (spatial organization), 124, 191.
- Cortico-caudate fibers. *See* Fibers.
- Cortico-fugal fibers. *See* Fibers.
- Cortico-geniculate fibers. *See* Fibers.
- Cortico-nigral fibers. *See* Fibers.
- Cortico-pallidal fibers. *See* Fibers.
- Cortico-peduncular fibers. *See* Fibers.
- Cortico-rubral fibers. *See* Fibers.
- Cortico-tectal fibers. *See* Fibers.
- Cortico-thalamic fibers. *See* Fibers.
- Corti's organ, 93, 95.
- Decentralistic concept of brain organization. *See* Brain, 3, 166, 186, 187, 196, 197, 206, 215, 217.
- Degeneration of cells, retrograde (Nissl), 19, 129, 143.
- Differentiation of central region of hemisphere. *See* Cortex.
- Dissonance (in audition), 99, 100.
- Distance receptors, 222, 223.
- Double projection of Macula. *See* Macula; Unilaterality.
- Dynamists, dynamic. *See* Brain, 196.
- Efferent fibers. *See* Fibers.
- Environment, surrounding world, 219, 223.
- Equipotentiality, areal (Lashley). *See* Brain, 217.
- Equipotentiality of cerebral cortex. *See* Brain, 3, 215.
- Equivalence of cerebral cortex. *See* Brain, 3, 215.
- Ewald's theory of hearing, 93.
- Experiment I, 27, 28, 108, 231-248.
- Experiment II, 32, 33, 56, 113, 249-267, 270.
- Experiment III, 38, 39, 118, 271-279.
- Experiment IV, 121, 280, 281.
- Experiment V, 282.
- Experiment V-A, 42, 43, 45, 125, 126.
- Experiment V-B, 129, 130, 131, 132.
- Experiment V-C, 134, 135, 140.
- Experiment V-D, 143, 144.
- Experiment V-E, 147, 148.
- Experiment VI, 213, 268, 269, 282.
- Experiment VII, 213, 283, 284.
- Experiment VIII, 213, 285-289.
- Experiment IX, 290.

Index

- Experiment XIV, 196, 213, 216, 291-299.
Experiment XV, 213, 300, 301.
Eye movements (conjugate), 175, 213.
Eye reflexes (protective), 137, 149, 194.
Fasciculus arcuatus corporis geniculati lateralis (Ferraro), 143.
Fasciculus corporis callosi cruciatus (Niessl von Mayendorf, R. A. Pfeifer). *See* Fibers, 14, 74, 108, 143, 147, 157, 179, 182.
Fasciculus longitudinalis inferior, 157.
Fibers, afferent auditory. *See* Radiation.
Fibers, afferent somato-sensory. *See* Radiation.
Fibers, afferent visual. *See* Radiation.
Fibers, associational of precentral cortex (terminations), 268, 269.
Fibers, associational of striate area, 196, 206, 216, 291-299.
Fibers, auditory (terminations), 81, 87, 88, 89.
Fibers, cochlear (direct), 95, 96, 97, 98.
Fibers, cochlear (spiral), 94, 97, 98.
Fibers, cortico-caudate, 70, 249, 283, 285, 286, 288, 290.
Fibers, cortico-fugal, 70, 71.
Fibers, cortico-fugal postcentral, 213, 282.
Fibers, cortico-fugal precentral, 213, 283-287.
Fibers, cortico-fugal of striate area, 213.
Fibers, cortico-nigral, 72, 288, 289.
Fibers, cortico-pallidal, 72, 283, 284, 286, 287.
Fibers, cortico-peduncular, 72, 288, 289.
Fibers, cortico-rubral, 72, 290.
Fibers, cortico-tectal (occipital), 162, 213, 300, 301.
Fibers, cortico-thalamic, 25, 71.
Fibers for light reflex, 25.
Fibers, intrathalamic, 23, 25.
Fibers, macular. *See* Cortex; Fasciculus corporis callosi cruciatus; Macula; Macular path; Radiation, 126, 169.
Fibers, peripheral optic, 162.
Fibers, radiated, of cortex, 153, 268, 269.
Fibers, somato-sensory (cortical terminations), 53, 56, 76, 263-267.
Fibers, thalamo-cortical. *See* Radiation.
Fibers, thalamo-striate, 29.
Fibers, visual (cortical terminations), 153, 199, 262, 270, 278.
Fields, visual. *See* Visual fields.
Figures (configurations) of Gestalt-psychology, 94, 108, 134, 142, 143, 191, 195, 196, 197, 217, 218.
Fissura calcarina, 163, 165, 177, 212.
Fissura calcarina (lower lip), 171.
Fissura calcarina (upper lip), 169.
Flechsig's concept of cerebral organization, 213, 214.
Focal or nuclear zone. *See* Cortex.
Fovea centralis corticalis, 178, 204.
Fovea centralis of macula lutea, 176.
Function of auditory system, 92, 94-102.
Function of macular cortex, 217, 218.
Function of postcentral cortex, 66-69.
Function of precentral cortex, 66-69.
Function of somato-sensory cortex, 66-69, 73, 77.
Function of somato-sensory radiation, 66, 73.
Function of visual system, 145, 149, 161, 183, 189, 192, 193.
Function of visual system (higher), 206.
Functional segmentation of cerebral cortex, 64, 67, 73.
Functional segmentation of thalamo-cortical radiation, 73.
Functional segmentation of thalamus, 73.
Geniculate body (external, lateral), 15, 130, 132, 138, 140, 142, 146, 151, 157, 162, 193.
Geniculate body, external (macular segment), 147.
Geniculate body (intercalated neurons). *See* Neurons.
Gennari's or Vieq d'Azyr's stripe. *See* Cortex.
Gesichtsfeldrest. *See* Remnant.

Index

- Gestalt-psychology. *See* Figures, Whole.
- Gustatory system, 214.
- Hair cells of cochlea, 95.
- Harmony (in addition), 99, 100.
- Hearing (theories). *See* Ewald, Helmholtz, Rutherford, 92-102.
- Hearing (scheme), 97.
- Helmholtz' theory of hearing, 92, 94, 100.
- Hemianaesthesia, 74.
- Hemianopsia (erescentic), 185, 186.
- Hemianopsia homonymous), 15, 134, 136, 137, 145, 146, 149, 150, 151, 164, 178, 179.
- Hemianopsia (homonymous bilateral), 187.
- Hemianopsia (homonymous complete), 181, 182.
- Hemianopsia (homonymous incomplete), 181, 182.
- Hemianopsia (homonymous macular, central), 182, 185, 188.
- Hemianopsia (macular, central), quadrant superior, inferior, 185.
- Hemianopsia (bilateral) quadrant superior, inferior, 183, 184, 187.
- Heschl's transverse temporal convolution, 84, 89, 90, 103, 234, 235, 254, 255.
- Individual (internal world), 224.
- Integration (in cerebral cortex), 192, 196, 207.
- Intercalated nerve cells. *See* Neurons.
- Isolation of elementary units in visual system, 191, 192, 194, 197.
- Klüver's experiments on vision in monkeys, 218.
- Lashley's areal equipotentiality, 217.
- Lenniseus (direct, cortical), 70.
- Limes parastriatus gigantopyramidalis, 166, 198, 200.
- Local signs or signatures, 95, 191.
- Localistic concept of brain organization, 211, 213-218.
- Localization, cerebral (principle), 2, 14, 15, 73, 93, 190, 193, 194, 197, 205, 213, 217.
- Localization (visual), 136.
- Macula (bilateral or double projection). *See* Unilaterality, 14, 15, 160, 178, 179, 180, 182, 183, 204.
- Macula (functional), 178.
- Macula lutea of retina, 173, 177.
- Macula (quadruple projection), 183.
- Macular cortex. *See* Cortex.
- Macular cortex (association connections). *See* Fibers.
- Macular fibers. *See* Macular path.
- Macular hemianopsia. *See* Hemianopsia.
- Macular path (bundle), 14, 108, 109, 110, 111, 112, 125, 126, 127, 128, 129, 159, 169, 171, 177, 180.
- Macular projection upon cortex, 182, 203.
- Macular projection (multilocular), 204.
- Macular quadrants (projection), 171.
- Macular (central) vision, 14, 15, 176, 177.
- Macular (central) vision (preservation or sparing in hemianopsia), 15, 164, 179, 180, 181, 182, 183.
- Macular (central) vision (preservation in hemianopsia [explanation]), 180.
- Marchi method, 19.
- Meshwork (basal in cortex), 156.
- Mosaic of elementary units (visual), 191, 193, 195.
- Motor cortex, 5, 66, 67, 68.
- Movements of Eyes. *See* Eye.
- Nervous system, central (biological significance), 220.
- Nervous system (diffuse), 221.
- Neurons (condensation, isolation), 222.
- Neurons, intercalated or associational (in external geniculate body), 108, 143, 147, 151, 152, 192.
- Neurons (rearrangement), 221.
- Neurons (spatial arrangement), 222, 226.
- Nissl's retrograde degeneration. *See* Degeneration.
- Nuclear or focal zone. *See* Cortex.
- Occipital operculum, 165, 169, 170, 173, 178, 212.
- Olfactory system, 214.

Index

- Omnipotentiality (areal). *See* Lashley.
- Omnipotentiality (cerebral). *See* Decentralistic concept; Brain.
- Omnivalence of cerebral cortex. *See* Decentralistic concept; Brain.
- Organization of afferent pathways (biological significance), 219-226.
- Organization (internal of auditory radiation). *See* Radiation.
- Organization (internal of somatosensory radiation). *See* Radiation.
- Organization (internal of visual radiation). *See* Radiation.
- Organization (internal of visual system). *See* Visual system.
- Organization (spatial of afferent pathways). *See* Afferent paths.
- Organization (spatial of visual cortex). *See* Cortex.
- Organization (spatial of visual system). *See* Visual system.
- Peri-parastriate area. *See* Area peri-parastriata.
- Pictures. *See* Figures, Whole.
- Postcentral cortex. *See* Cortex.
- Posterior horn. *See* Ventricle.
- Praegeniculate. *See* Corpus.
- Precentral cortex. *See* Cortex.
- Principle of localization. *See* Localization.
- Principle of neighborhood, 117, 161, 192, 197.
- Principle (spatial), 161, 190, 191, 192.
- Processes (elementary, cerebral), 218.
- Processes (higher, composite, cerebral), 225.
- Processes (higher, visual), 206, 218.
- Projection areas (cerebral). *See* Areas.
- Projection areas in monkey (scheme), 212.
- Projection of cochlea, cerebral. *See* Cochlea.
- Projection of macula, bilateral. *See* Macula.
- Projection of retina. *See* Retina.
- Projection of retina (point-to-point). *See* Retina.
- Projection of retina (cortical [scheme]). *See* Retina.
- Pseudomacula, 178.
- Radiated fibers (bundles) in cortex. *See* Fibers.
- Radiation, auditory, internal geniculocortical. *See* Unilaterality, 81, 101, 102, 103, 163.
- Radiation, auditory (internal organization, segmentation), 81, 84, 85, 101, 104.
- Radiation (Gratiolet), 164.
- Radiation, somato-sensory (organization, segmentation), 73.
- Radiation, somato-sensory, thalamocortical. *See* Unilaterality, 27, 72, 73, 74, 114, 163, 199.
- Radiation, visual (boundary bundles), 115, 119, 123, 124, 158.
- Radiation, visual (dorsal horizontal branch), 167.
- Radiation, visual, external geniculocortical. *See* Macular path; Unilaterality, 12, 107, 157, 162, 199, 205.
- Radiation, visual (intermediate or perpendicular branch), 126, 169.
- Radiation, visual (internal organization, segmentation), 117, 142, 158, 167, 172, 189, 199, 201, 205.
- Radiation, visual (spatial organization), 158.
- Radiation, visual (threefold subcortical origin), 162, 205.
- Radiation, visual (ventral horizontal branch), 170.
- Reduction of visual fields (circular). *See* Visual fields.
- Reflexes, visual. *See* Eye.
- Remnant of visual fields. *See* Visual fields.
- Rests of visual fields (triangular). *See* Visual fields.
- Retina (cerebral projection), 12, 15, 159, 160, 166, 168, 172, 173, 174, 175, 182, 187, 190, 202, 203.
- Retina, cerebral projection (diffuse, unstable), 205.

Index

- Retina, cerebral projection (scheme), 168, 174.
- Retina, cerebral projection (three-fold), 200, 204.
- Retina (geniculate projection), 15, 167, 174, 193, 202, 203.
- Retina (geometric, mathematical projection), 205, 207.
- Retina (point-to-point projection), 178, 182, 190, 217.
- Retina (projection upon visual radiation), 158, 167, 168, 174, 201, 202, 203.
- Retinal quadrants (projection), 172, 174.
- Retrocalcarina, 181.
- Retrograde degeneration. *See* Degeneration.
- Rutherford's theory of hearing, 93, 94.
- Schaltzellen. *See* Neurons.
- Scotoma, 15, 136, 177, 179, 185, 188, 201.
- Scotoma (homonymous extramacular), 185.
- Scotoma (homonymous macular, central), 185.
- Scotoma (peripheral extramacular, multiple), 186.
- Scotoma (semicircular), 188.
- Segmentation of auditory cortex. *See* Cortex.
- Segmentation of auditory radiation. *See* Radiation.
- Segmentation of somato-sensory cortex. *See* Cortex.
- Segmentation of somato-sensory radiation. *See* Radiation.
- Segmentation of thalamus. *See* Thalamus.
- Segmentation of visual cortex. *See* Cortex.
- Segmentation of visual radiation. *See* Radiation.
- Sensations (elementary auditory), 96.
- Sensibility (exteroceptive), 67, 68.
- Sensibility (localization in cortical areas and layers), 67, 68.
- Sensibility (primitive or elementary qualities), 68.
- Sensibility (proprioceptive), 67, 88.
- Sensibility (unconscious reflex s.), 67, 68.
- Sensomotorium, 66.
- Sensory-motor region of cerebral cortex, 5, 64, 66.
- Similarity of octaves (in audition), 97, 99.
- Somatic sensory cortex. *See* Cortex.
- Somato-sensory radiation. *See* Radiation.
- Somato-sensory system, 5, 21, 70.
- Somato-sensory system (function). *See* Function.
- Somato-sensory system (pathology), 66, 74.
- Space, visual (perception), 191.
- Sparing of macular or central vision. *See* Macular vision.
- Sparing of sensation, 74.
- Spatial organization of afferent pathways. *See* Afferent paths.
- Stimuli, external, and afferent systems, 219, 220.
- Stimuli (spatial properties), 221, 222, 224, 225.
- Stimuli (visual), 191.
- Stratum extremum, 110, 123.
- Stratum sagittale externum (laterale), 157, 163, 199.
- Stratum sagittale internum, 157, 163, 199.
- Striate area. *See* Cortex.
- Sulcus calcarinus externus, s. occipitalis superior, 127, 178, 204, 212.
- Sulcus centralis, 45, 48, 55, 56, 61, 63, 75, 212, 263, 264, 265, 266, 267.
- Sulcus cinguli, 212.
- Superior colliculus. *See* Colliculus.
- Surrounding world. *See* Environment.
- Sylvian area (posterior), 87, 90, 103, 212.
- Sylvian fissure (fossa), 212.
- Tapetum, 157, 163, 164, 199.
- Terminations of association fibers in precentral cortex. *See* Fibers.
- Terminations of auditory fibers in cortex. *See* Fibers.
- Terminations of somato-sensory fibers in cortex. *See* Fibers.

Index

- Terminations of visual fibers in cortex. *See* Fibers.
- Thalamo-cortical radiation. *See* Radiation.
- Thalamo-striate fibers. *See* Fibers.
- Thalamus, 23, 162.
- Thalamus (internal organization, segmentation), 67, 70, 73.
- Time, visual (perception), 191.
- Total, totalizing function, 192, 195, 196, 207.
- Tract (tractus). *See* Fibers, Radiation.
- Transverse temporal convolution of Heschl. *See* Heschl.
- Unilaterality of auditory radiation, 86, 102.
- Unilaterality of somato-sensory radiation, 73, 74.
- Unilaterality of visual radiation, 113, 115, 120, 124, 127, 143, 144, 147, 151, 152, 157, 160, 164, 179, 180, 199, 204.
- Units, elementary, in visual system, 191.
- Unity of higher visual processes, 207.
- Ventricle, lateral (posterior horn), 163.
- Vieq d'Azyr's stripe. *See* Cortex.
- Vision, central. *See* Macular vision.
- Vision (stereoscopic), 183.
- Visual fields (circular reduction), 188.
- Visual fields (hemianopsia). *See* Hemianopsia.
- Visual fields (remnant), 179.
- Visual fields (scotoma). *See* Scotoma.
- Visual fields (triangular rests), 188.
- Visual path. *See* Radiation, Retina, Visual system.
- Visual radiation. *See* Radiation.
- Visual system, 12, 105, 107, 199.
- Visual system (finer organization, general), 189.
- Visual system (function). *See* Function.
- Visual system (internal organization), 161, 187, 189, 191, 192, 193, 205.
- Visual system (pathology), 183.
- Visual system (scheme), 168, 174.
- Visual system (spatial organization), 191, 192, 205.
- Whole, in visual perception, 192, 195, 196, 207.

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Index. Pp. 545-551.	
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