# EXTERNAL MORPHOLOGY

OF

# THE PRIMATE BRAIN

By

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# FOREWORD

THIS TIMELY book is a well coördinated series of studies dealing with the development of cortical fissuration of the primate brain. The work is the result of a long study and much personal experience with well-preserved and documented material. No pains have been spared to utilize the specimens of brains in a most exacting scientific way. The perceptual data required for such a synthesis were too complex to be retained without the use of numerous photographs, tracings, diagrammatic records, and the selection of proper sequences for purposes of presentation. There is no confusion or devious argument in this work. The author has presented the findings and conclusions in a systematic and logical way which will win the gratitude of the interested reader.

This work is based on ample material on every important stage of cortical development from lemur to man. Mere sampling has been studiously avoided and original gaps have been filled at numerous points. The fundamental primate pattern of cortical expansion has been traced and substantiated at every stage. Variations within the species and between different species have been explored. There is a remarkable consistency in this work because it is based on a single aspect of brain morphology without attempt to use other and less complete data.

Doctor Connolly shows that amid complexity and variety in every primate stage there is still a constant and persistent surface pattern of the cortex. The progressive expansion of every sulcus and gyrus can be clearly traced step by step from the less to the more convoluted brains. The process, though variable in individual cases, is never fortuitous, but always logical. Severe regressions are seldom seen in the normal brain. There is revealed in normal brains a certain law of sequences which inexorably leads in the direction of greater growth and expansion of certain newer functional areas. With this there is a constant emergence of more of the gyri or new ones, and separation, lengthening and shifting of the sulci. The book presents in a lucid way the surface evidence of this progressive unfolding and dynamics of growth of the primate cortex.

At times it is evident that variations in sulci dominate over size. Many new expansions of cortex express themselves early and in small forms. These may be departures not seen in older brains. It seems clear that the expressions of genetic process of brain growth appear early in life and are not as a rule carried further in the adult stage of development. Genetic determinism with a variation toward advanced steps of development may thus sometimes be seen in brains of young individuals.

Within the species the size alone does not determine the complexity of cortical fissuration. In some instances a smaller brain may have a more advanced fissuration. But, generally, the brains of larger species are more advanced along the same lines than those of smaller species.

This book is richly documented. It is a reliable study of considerable scope the like of which has not appeared in recent times. Doctor Connolly's exposition is always clear and as brief as the subject will allow. It is well illustrated and substantiated by observations of outstanding dependability. It has the merit of clarifying a number of special problems. Many errors and hasty misconceptions which have found their way into older and recent literature have been carefully studied and corrected. The entire series of homologies in the frontal, parietal, and occipital cortices have been carefully reviewed from new material. As a result many of the old views have been validated; and interpretations of the development of some of the newer cortical formations have been corrected and the progressive changes brought into clear relief by the author's painstaking efforts.

The results obtained from the study of endocranial casts and the corresponding brains of modern man will be of value in the interpretation of the fissural markings on the endocranial casts of prehistoric man.

This timely book has a certain prognostic value for the future in brain research. The studies of the brain suggest a relation of growth of sulci and gyri to the expansion of differing histologic areas of the cortex and to the growth of thalamocortical radiations from thalamic nuclei to the cortex. In these phenomena there may lie a fresh and broader approach to the understanding of cortical localization on a more complete morphological basis. We may predict that in the future we need not stop with a meager localization of the sensory and the motor areas alone, but may go on to a broader basis of localization founded on a larger number of projection areas of nearly all the thalamic nuclei. Furthermore, the study of intracortical connections may lead us to a better understanding of local as well as transcortical functions of the brain.

*Cornell University*

JAMES W. PAPEZ, M.D.

# PREFACE

SOMETIME AGO it was suggested by several of my friends among the scientists, that it would be useful to have in collected form the researches on the fissural pattern of the brain, which were published in the American Journal of Physical Anthropology. The studies were carried out intermittently over a considerable period of time as opportunity afforded. On account of the shortage of paper in the recent disturbed years, the republication of the researches without revision did not seem to me warranted, and I followed through with new studies on the development of the fissures of the brain and experimental studies on the problem of fissural representation on endocranial casts of anthropoids and man.

In the meantime new literature relating to the subject appeared and this would require consideration in any republication. While the findings in this new literature did not modify my interpretation, it was obvious that great differences of opinion still existed regarding the true interpretation of the fissural pattern of some parts of the anthropoid brain in comparison with the human brain. Without pretense of finality, but to clarify further the interpretations which were based on observations of extensive material, I thought it advisable to revise the entire series and to add new illustrative material bearing on the interpretations previously given.

These revised studies have been integrated with the new studies which make up the second half of the book. While these latter studies are independent, the interpretations to be found there are based on ample illustrative material in the earlier studies and frequent references are made to the figures illustrating developmental stages, which it is hoped, will prove useful to the reader.

In the preparation of the revised and new studies which make up this book, I have had the good fortune of consulting the distinguished neuroanatomists, Professors James W. Papez and Gerhardt von Bonin, both of whom, apart from their numerous papers in their special field, have made valuable contributions to the anthropology of the brain. Doctor Papez, who read all of the previously published studies as well as the new ones, made valuable critical comments and suggestions as to the further elaboration of the text and has written a generous Foreword, for which I am very grateful. Doctor von Bonin gave a critical reading of the previously published papers and some of the revised ones and made very useful suggestions as to further comparisons of typical genera. He has also drawn my attention to some literature which otherwise I should have neglected. In the endeavor to carry out these suggestions, I hope that as a result the book has been made more useful.

I am also indebted to my colleague, Doctor James Van der Veldt of the Psychology and Psychiatry Department of the University for a careful reading of

the text in its final form. Acknowledgment is also due to Sr. M. Clodine, graduate student, for much assistance in preparing and integrating the text for publication.

The studies were made on the brain collection in the United States National Museum, Division of Physical Anthropology. I am greatly indebted to the Smithsonian Institution for permission to study this fine collection. Especially to Doctor T. Dale Stewart, Curator of the Division of Physical Anthropology, I am grateful for his unfailing courtesy and his affording me every facility, while carrying on the work during the period since the passing of his distinguished predecessor, Aleš Hrdlička. Doctor Stewart has also made many helpful suggestions concerning the publication of these studies. For additional material included in the investigations, acknowledgement is made in the separate studies.

I wish to thank the Wistar Institute of Anatomy and Biology for permission to republish the figures which originally appeared in the American Journal of Physical Anthropology and for Figure 333 after Davidson Black. Also gratefully acknowledged is the permission from the Cambridge University Press, England and the Macmillan Co., New York, to republish Figure 58, after Campbell; from Mme. C. von Economo for Figure 282; from the Netherlands Academy of Science, Amsterdam, for Figures 331 and 332 after Dubois and Figure 334 after Kappers and Bouman; and from *L'Anthropologie*, Mason et Cie, Paris, for Figures 336 and 337, after Boule and Anthony.

Finally, I should like to express my sincere thanks to the publisher, Charles C Thomas and to his associates, for their cooperation and for the care that they have taken in the production of this book in accordance with their usual high standards.

*Washington, D. C.* CORNELIUS J. CONNOLLY

## ABBREVIATIONS

*For all figures of primate brains including the human when the sulci are present*

S, fissura Sylvii seu lateralis
R, ramus ascendens fissurae Sylvii
R′, ramus horizontalis fissurae Sylvii
c, s. centralis
pcs, s. praecentralis superior
pcm, s. praecentralis medius
pci, s. praecentralis inferior
h, ramus horizontalis pci
fs, s. frontalis superior
fm, s. frontalis medius
fi, s. frontalis inferior
d, s. diagonalis
r, s. rectus
W, s. fronto-marginalis
ol, s. olfactorius
o, s. orbitalis
fo, s. fronto-orbitalis
sf, s. subfrontalis
io, incisura opercularis
rp, f. rhinalis posterior
sca, s. subcentralis anterior
scp, s. subcentralis posterior
pts, s. postcentralis superior
ptm, s. postcentralis medius
pti, s. postcentralis inferior
ptr, s. postcentralis transversus
ip, s. intraparietalis
e, processus acuminis s. intraparietalis
ps, s. parietalis superior
ina, s. intermedius anterior
inp, s. intermedius posterior
ts, s. temporalis superior
tm, s. temporalis medius
oct, s. occipito-temporalis
seu ti, s. temporalis inferior
oci, s. occipitalis inferior
L, s. lunatus
pl, s. praelunatus
par, s. paroccipitalis
otr, s. occipitalis transversus
po, f. parieto-occipitalis
ipo, incisura parieto-occipitalis
lp, s. limitans praecunei
cm, s. callosomarginalis
rs, s. rostralis
sp, s. subparietalis
pm, s. paramedialis
ca, rc, pc, s. calcarinus, retrocalcarinus, paracalcarinus
lc, s. calcarinus lateralis
u, ramus superior lc.
$a^1$, $a^2$, $a^3$, rami ts.

*For other abbreviations, especially for Figures 1, 2, and 4, see text.*

# CONTENTS

# EXTERNAL MORPHOLOGY
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I

# THE FISSURAL PATTERN OF THE PRIMATE BRAIN

## INTRODUCTION

MANY INVESTIGATIONS have been made on the fissural pattern and convolutions of the primate brain and a very extensive literature exists on the subject. In many of the earlier studies the number of specimens available was very limited and numerous papers describe but a single specimen as representative of a whole group. That situation was naturally to be expected when material was scarce.

There are, however, excellent comparative studies in which fairly large series of brains representing many genera of primates have been investigated, such as those of Gratiolet, Kükenthal and Ziehen, Kohlbrugge, Zuckerkandl, Anthony, Cunningham and Elliot Smith. G. Retzius has left us a volume of unsurpassed photographs of primate brains, though no text accompanies the photographs except in the case of the lower primates.

Even in the larger comparative investigations, the material representing some genera is very limited, or it may be entirely wanting, and further studies filling in some of the gaps seem therefore desirable.

There are further reasons, however, which lead the writer to examine anew the various groups of primate brains. Some interpretations quite well established by the great brain anatomists have been overlooked in more recent investigations. These need reaffirmation on the basis of further observation. Again it happens that on some rather important points, the anatomists have not come to an agreement on the interpretation of the observed conditions. This is no doubt due to defective material or lack of sufficient material. Further independent observations on adequate material should throw some light on these points and aid in deciding the true interpretation.

Again in the comparative studies of the sulci hitherto made, only isolated comparisons were made of fetal and adult brains; and in some large series both the approximate age and sex of the animals to which the brains belonged were unknown, so that differences, possibly due to these factors, could not be considered. The influence of age, however, is not easy to determine as some 'young' specimens are larger and heavier than some adult specimens of the same species. Further the percentage of the mature size of the brain already attained at birth in infra-human species is quite high and the period of growth relatively shorter than in the human brain. Comparison will therefore be made especially of the very young brain with that of the adult and size or weight of brain considered in the case of adolescents.

Baillarger (1845) made the observation that the surface of the human brain, relative to its volume, is less than in the lower mammals. In more general terms, larger brains have relatively less surface extent than smaller brains. This he noted follows from the geometric law of volumes that the volume increases as the cube of the diameter while the surface increases as the square. To compensate for this, larger brains tend to have more folding of the cortex or fissuration than smaller brains of the same order. Dareste (1862) further developed this concept and noted that even with increased fissuration, the size of the cortex is relatively smaller in larger than in smaller brains.

The number of brains included in the following studies affords an opportunity to observe any influence of size or weight on fissuration in the various families of the primate order. But irrespective of the number of sulci present, the sulcal pattern, though basically the same, differs considerably in the different groups, so that an array of specimens according to a sulcal pattern exhibiting various degrees of differentiation of the cortex may be quite different from an array according to the number of sulci present. This differentiation of the cortex is indicated by the form and position of the sulci and the appearance in the ascending series of new sulci which are important in that they become established and limit fixed gyral entities. The sulcal pattern exhibiting this differentiation is of much interest in the light of the position given to a group on other anatomical grounds. As in the human brain, however, both young and adult show much variability in this degree of differentiation, but the variability does not transcend certain limits in the various groups, especially in sub-families.

The interpretation of the sulci of the frontal lobe has always presented difficulties, especially in the case of anthropoids. Practically every possible interpretation has been given by the earlier investigators in making comparisons with the human brain. A new inferior frontal sulcus, however, appearing first in the ascending series in specimens of the large anthropoid brain, does not seem to have been recognized by the early investigators.

Retzius (1906) did not label an inferior frontal sulcus in any figure of the anthropoid brain, nor does he interpret all of the sulci of the inferior frontal region. The investigations of Zuckerkandl (1902 to 1906) and especially of Kohlbrugge (1903) caused Retzius to proceed no further with his manuscript of the text planned to accompany the plates of his work and he modified his views regarding some of the sulci already labeled in the figures.

Kohlbrugge investigated 106 hemispheres including Hylobates (2 species), Semnopithecus (4 species), Macaca (3 species), Cercocebus (one species) and Cercopithecus (one species), and found great variability. He came to the conclusion that not a single sulcus nor the form of a sulcus is characteristic of a particular genus, and that one can speak only of frequencies. He separated, however, Hylobates and Semnopithecus as a group distinguished from a second group embracing all other genera investigated. Retzius accepted this conclusion and was no longer convinced of Gratiolet's view (1854) that a typical arrangement of sulci and gyri existed in the various groups of ape brains.

One may accept Kohlbrugge's conclusion based on his limited number of genera, of which, however, at least two groups are distinguished among five genera, and yet from a different approach find important differences between genera. The presence or absence of some sulcus or the form of any sulcus, may not be characteristic of a genus, yet the combination or pattern of sulci may be characteristic. Granting the great similarity in the brains of the Cercopithecidae, one could say that the sulcal pattern of Semnopithecus (Presbytis) never attains the degree of differentiation shown in some specimens of Hylobates, so that on this basis there are at least three groups in the above five genera. A similar approach will enable one to distinguish the brains of some other genera, though not all and it must further be considered that some genera are not accepted as well authenticated by all taxonomists.

Evidence will be presented in the following studies, showing various degrees of differentiation of cortical areas in the different groups. The varying degree of differentiation is also exhibited within a genus and it is by observing the genesis of new sulci and the destiny of offshoots of sulci that light is thrown on their significance. This is illustrated especially in the inferior frontal region of the large anthropoids which shows varying degrees of development. The observations of a sequence in the appearance and development of sulci, it is hoped, will help to elucidate the sulcal configuration in this and other regions of the brain.

The literature cited in the course of these studies, pertains mainly to works of a comparative nature. Elliot Smith (1903) and Kükenthal and Ziehen (1895) review the earlier literature and an extensive bibliography is given by Ariëns Kappers, Huber and Crosby (1936).

## MATERIAL INVESTIGATED

The material of this investigation is the Hrdlička Collection of the U. S. National Museum, Division of Physical Anthropology and constitutes one of the largest existing collections of primate brains. They are with few exceptions excellently preserved and reveal the true form of the brain. In a large percentage of cases the brains were extracted by the late Doctor Hrdlička with his wonted care. Much of the anthropoid and Cercopithecidae material is from animals collected in the field by the late Dr. W. L. Abbot who made records of the sex and approximate age.

The number of complete infra-human brains studied was 330 or 660 hemispheres representing over fifty species from lemurs to anthropoids inclusive.

The names of the species and number of specimens representing each are given under the genus heading, and also the sex and approximate age, fetal, young or adult. Within the age group, brain weights will be considered in comparing the stage of development of the fissural pattern especially in the higher Primates.

In regard to nomenclature a difficulty presents itself in that authorities in primate classification are not in agreement. Elliot's work (1913), though widely used, has not received full approval. Papers have been consulted on special groups such as lemurs by Schwarz (1931), macaques by Miller (1933) and gibbons by Schultz (1933). To avoid ambiguity, synonyms are given in the case of some genera and species and with the additional use of popular names, the species of animal whose brain is described will be recognized.

Before removing the meninges from the specimens, projectional measurements were taken of the hemispheres and their parts.

The figures represent approximately the true form of the brain. The outlines of the specimens, giving in most cases a lateral view, were either traced by the writer from photographs made with the midsagittal plane parallel to the camera plate, or by means of an adaptation of the stereograph to be described later. The sulci were also traced in part. Those near the medial border are of course not seen distinctly in a lateral view by this projectional method. To avoid the multiplication of figures by the addition of dorsal views in all cases, the sulci near the border were drawn proportionately downward, so the configuration of the sulci and their relations to one another are seen in one view in the figures. The points of incision of the central sulcus and the parieto-occipital show their true projectional relations to the frontal and occipital poles of the brain. The writer is indebted to the Smithsonian photographers, Mr. G. I. Hightower and Mr. F. B. Kestner, for the care they have taken in making the photographs.

More attention was formerly given to a description of the convolutions and their relations than to the fissures, the former being considered primary. Irrespective of that problem, a more precise description can be given by describing the fissural relations. The relative size of the convolutions and their interconnections can be judged from the figures and only in special cases such as the submergence or emergence of convolutions need attention be drawn to them.

Reference is made frequently in the following studies to the underlying cortical areas as described by the brain histologists and to the relationship that may exist between these areas and the sulci. The evidence for any relationship will be discussed at the end of these studies. In any case it is desirable to identify the sulci in cortical studies so that one may be oriented in the inspection of brain maps. The sulci could serve as reference charts. But even were no definite relation found to exist between sulci and cortical areas, which is improbable, there would still remain a biological problem: Why the sulci? For the sulci are not a haphazard or chaotic occurring phenomenon but appear with remarkable constancy and with very definite relations to one another and to the brain as a whole.