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NOTE ON THE RESEMBLANCES AND DIFFERENCES IN THE STRUCTURE AND THE DEVELOPMENT OF THE BRAIN IN MAN AND APES

BY

PROFESSOR T. H. HUXLEY, F.R.S.

[This essay is taken from 'The Descent of Man and Selection in relation to Sex' by Charles Darwin where it appears at the end of Chapter VII which is also the end of Part I. Footnotes are numbered as they appear in 'The Descent of Man.']

The controversy respecting the nature and the extent of the differences in the structure of the brain in man and the apes, which arose some fifteen years ago, has not yet come to an end, though the subject matter of the dispute is, at present, totally different from what it was formerly. It was originally asserted and re-asserted, with singular pertinacity, that the brain of all the apes, even the highest, differs from that of man, in the absence of such conspicuous structures as the posterior lobes of the cerebral hemispheres, with the posterior cornu of the lateral ventricle and the hippocampus minor, contained in those lobes, which are so obvious in man.

But the truth that the three structures in question are as well developed in apes' as in human brains, or even better; and that it is characteristic of all the Primates (if we exclude the Lemurs) to have these parts well developed, stands at present on as secure a basis as any proposition in comparative anatomy. Moreover, it is admitted by every one of the long series of anatomists who, of late years, have paid special attention to the arrangement of the complicated sulci and gyri which appear upon the surface of the cerebral hemispheres in man and the higher apes, that they are disposed after the very same pattern in him, as in them. Every principal gyrus and sulcus of a chimpanzee's brain is clearly represented in that of a man, so that the terminology which applies to the one answers for the other. On this point there is no difference of opinion. Some years since, Professor Bischoff published a memoir (70. 'Die Grosshirn-Windungen des Menschen;' 'Abhandlungen der K. Bayerischen Akademie,' B. x. 1868.) on the cerebral convolutions of man and apes; and as the purpose of my learned colleague was certainly not to diminish the value of

the differences between apes and men in this respect, I am glad to make a citation from him.

"That the apes, and especially the orang, chimpanzee and gorilla, come very close to man in their organisation, much nearer than to any other animal, is a well known fact, disputed by nobody. Looking at the matter from the point of view of organisation alone, no one probably would ever have disputed the view of Linnaeus, that man should be placed, merely as a peculiar species, at the head of the mammalia and of those apes. Both shew, in all their organs, so close an affinity, that the most exact anatomical investigation is needed in order to demonstrate those differences which really exist. So it is with the brains. The brains of man, the orang, the chimpanzee, the gorilla, in spite of all the important differences which they present, come very close to one another" (loc. cit. p. 101).

There remains, then, no dispute as to the resemblance in fundamental characters, between the ape's brain and man's: nor any as to the wonderfully close similarity between the chimpanzee, orang and man, in even the details of the arrangement of the gyri and sulci of the cerebral hemispheres. Nor, turning to the differences between the brains of the highest apes and that of man, is there any serious question as to the nature and extent of these differences. It is admitted that the man's cerebral hemispheres are absolutely and relatively larger than those of the orang and chimpanzee; that his frontal lobes are less excavated by the upward protrusion of the roof of the orbits; that his gyri and sulci are, as a rule, less symmetrically disposed, and present a greater number of secondary plications. And it is admitted that, as a rule, in man, the temporo-occipital or "external perpendicular" fissure, which is usually so strongly marked a feature of the ape's brain is but faintly marked. But it is also clear, that none of these differences constitutes a sharp demarcation between the man's and the ape's brain. In respect to the external perpendicular fissure of Gratiolet, in the human brain for instance, Professor Turner remarks: (71. 'Convulsions of the Human Cerebrum Topographically Considered,' 1866, p. 12.)

"In some brains it appears simply as an indentation of the margin of the hemisphere, but, in others, it extends for some distance more or less transversely outwards. I saw it in the right hemisphere of a female brain pass more than two inches outwards; and on another specimen, also the right hemisphere, it proceeded for four-tenths of an inch outwards, and then extended downwards, as far as the lower margin of the outer surface of the hemisphere. The imperfect definition of this fissure in the majority of human brains, as compared with its remarkable distinctness in the brain of most Quadrumana, is owing to the presence, in the former, of certain superficial, well marked, secondary convolutions which bridge it over and connect the parietal with the occipital lobe. The closer the first of these bridging gyri lies to the longitudinal fissure, the shorter is the external parieto-occipital fissure" (loc. cit. p. 12).

The obliteration of the external perpendicular fissure of Gratiolet, therefore, is not a constant character of the human brain. On the other hand, its full development is not a constant character of the higher ape's brain. For, in the chimpanzee, the more or less extensive obliteration of the external perpendicular sulcus by "bridging convolutions," on one side or the other, has been noted over and over again by Prof. Rolleston, Mr. Marshall, M. Broca and Professor Turner. At the conclusion of a special paper on this subject the latter writes: (72. Notes more especially on the bridging convolutions in the Brain of the Chimpanzee, 'Proceedings of the Royal Society of Edinburgh,' 1865-6.)

"The three specimens of the brain of a chimpanzee, just described, prove, that the generalisation which Gratiolet has attempted to draw of the complete absence of the first connecting convolution and the concealment of the second, as essentially characteristic features in the brain of this animal, is by no means universally applicable. In only one specimen did the brain, in these particulars, follow the law which Gratiolet has expressed. As regards the presence of the superior bridging convolution, I am inclined to think that it has existed in one hemisphere, at least, in a majority of the brains of this animal which have, up to this time, been figured or described. The superficial position of the second bridging convolution is evidently less frequent, and has as yet, I believe, only been seen in the brain (A) recorded in this communication. The asymmetrical arrangement in the convolutions of the two hemispheres, which previous observers have referred to in their descriptions, is also well illustrated in these specimens" (pp. 8, 9).

Even were the presence of the temporo-occipital, or external perpendicular, sulcus, a mark of distinction between the higher apes and man, the value of such a distinctive character would be rendered very doubtful by the structure of the brain in the Platyrrhine apes. In fact, while the temporo-occipital is one of the most constant of sulci in the Catarrhine, or Old World, apes, it is never very strongly developed in the New World apes; it is absent in the smaller Platyrrhini; rudimentary in *Pithecia* (73. Flower, 'On the Anatomy of *Pithecia Monachus*,' 'Proceedings of the Zoological Society,' 1862.); and more or less obliterated by bridging convolutions in *Ateles*.

A character which is thus variable within the limits of a single group can have no great taxonomic value.

It is further established, that the degree of asymmetry of the convolution of the two sides in the human brain is subject to much individual variation; and that, in those individuals of the Bushman race who have been examined, the gyri and sulci of the two hemispheres are considerably less complicated and more symmetrical than in the European brain, while, in some individuals of the chimpanzee, their complexity and asymmetry become notable. This is particularly the case in the brain of a young male chimpanzee figured by M. Broca. ('L'ordre des

Again, as respects the question of absolute size, it is established that the difference between the largest and the smallest healthy human brain is greater than the difference between the smallest healthy human brain and the largest chimpanzee's or orang's brain.

Moreover, there is one circumstance in which the orang's and chimpanzee's brains resemble man's, but in which they differ from the lower apes, and that is the presence of two corpora candicantia—the *Cynomorpha* having but one.

In view of these facts I do not hesitate in this year 1874, to repeat and insist upon the proposition which I enunciated in 1863: (74. 'Man's Place in Nature,' p. 102.)

"So far as cerebral structure goes, therefore, it is clear that man differs less from the chimpanzee or the orang, than these do even from the monkeys, and that the difference between the brain of the chimpanzee and of man is almost insignificant when compared with that between the chimpanzee brain and that of a Lemur."

In the paper to which I have referred, Professor Bischoff does not deny the second part of this statement, but he first makes the irrelevant remark that it is not wonderful if the brains of an orang and a Lemur are very different; and secondly, goes on to assert that, "If we successively compare the brain of a man with that of an orang; the brain of this with that of a chimpanzee; of this with that of a gorilla, and so on of a *Hylobates*, *Semnopithecus*, *Cynocephalus*, *Cercopithecus*, *Macacus*, *Cebus*, *Callithrix*, *Lemur*, *Stenops*, *Hapale*, we shall not meet with a greater, or even as great a, break in the degree of development of the convolutions, as we find between the brain of a man and that of an orang or chimpanzee."

To which I reply, firstly, that whether this assertion be true or false, it has nothing whatever to do with the proposition enunciated in 'Man's Place in Nature,' which refers not to the development of the convolutions alone, but to the structure of the whole brain. If Professor Bischoff had taken the trouble to refer to p. 96 of the work he criticises, in fact, he would have found the following passage: "And it is a remarkable circumstance that though, so far as our present knowledge extends, there IS one true structural break in the series of forms of Simian brains, this hiatus does not lie between man and the manlike apes, but between the lower and the lowest Simians, or in other words, between the Old and New World apes and monkeys and the Lemurs. Every Lemur which has yet been examined, in fact, has its cerebellum partially visible from above; and its posterior lobe, with the contained posterior cornu and hippocampus minor, more or less rudimentary. Every marmoset, American monkey, Old World monkey, baboon or manlike ape, on the contrary, has its cerebellum entirely hidden, posteriorly, by the cerebral lobes, and possesses a large posterior cornu with a well-developed hippocampus minor."

This statement was a strictly accurate account of what was known when it was made; and it does not appear to me to be more than apparently weakened by the subsequent discovery of the relatively small development of the posterior lobes in the Siamang and in the Howling monkey. Notwithstanding the exceptional brevity of the posterior lobes in these two species, no one will pretend that their brains, in the slightest degree, approach those of the Lemurs. And if, instead of putting *Hapale* out of its natural place, as Professor Bischoff most unaccountably does, we write the series of animals he has chosen to mention as follows: *Homo*, *Pithecus*, *Troglodytes*, *Hylobates*, *Semnopithecus*, *Cynocephalus*, *Cercopithecus*, *Macacus*, *Cebus*, *Callithrix*, *Hapale*, *Lemur*, *Stenops*, I venture to reaffirm that the great break in this series lies between *Hapale* and *Lemur*, and that this break is considerably greater than that between any other two terms of that series. Professor Bischoff ignores the fact that long before he wrote, Gratiolet had suggested the separation of the Lemurs from the other Primates on the very ground of the difference in their cerebral characters; and that Professor Flower had made the following observations in the course of his description of the brain of the Javan *Loris*: (75. 'Transactions of the Zoological Society,' vol. v. 1862.)

"And it is especially remarkable that, in the development of the posterior lobes, there is no approximation to the Lemurine, short hemisphered brain, in those monkeys which are commonly supposed to approach this family in other respects, viz. the lower members of the *Platyrrhine* group."

So far as the structure of the adult brain is concerned, then, the very considerable additions to our knowledge, which have been made by the researches of so many investigators, during the past ten years, fully justify the statement which I made in 1863. But it has been said, that, admitting the similarity between the adult brains of man and apes, they are nevertheless, in reality, widely different, because they exhibit fundamental differences in the mode of their development. No one would be more ready than I to admit the force of this argument, if such fundamental differences of development really exist. But I deny that they do exist. On the contrary, there is a fundamental agreement in the development of the brain in men and apes.

Gratiolet originated the statement that there is a fundamental difference in the development of the brains of apes and that of man—consisting in this; that, in the apes, the sulci which first make their appearance are situated on the posterior region of the cerebral hemispheres, while, in the human foetus, the sulci first become visible on the frontal lobes. (76. "Chez tous les singes, les plis posterieurs se developpent les premiers; les plis anterieurs se developpent plus tard,

aussi la vertebre occipitale et la parietale sont-elles relativement tres-grandes chez le foetus. L'Homme presente une exception remarquable quant a l'epoque de l'apparition des plis frontaux, qui sont les premiers indiques; mais le developpement general du lobe frontal, envisage seulement par rapport a son volume, suit les memes lois que dans les singes:" Gratiolet, 'Memoire sur les plis cerebres de l'Homme et des Primateaux,' p. 39, Tab. iv, fig. 3.)

This general statement is based upon two observations, the one of a Gibbon almost ready to be born, in which the posterior gyri were "well developed," while those of the frontal lobes were "hardly indicated" (77. Gratiolet's words are (loc. cit. p. 39): "Dans le foetus dont il s'agit les plis cerebraux posterieurs sont bien developpes, tandis que les plis du lobe frontal sont a peine indiques." The figure, however (Pl. iv, fig. 3), shews the fissure of Rolando, and one of the frontal sulci plainly enough. Nevertheless, M. Alix, in his 'Notice sur les travaux anthropologiques de Gratiolet' ('Mem. de la Societe d'Anthropologie de Paris,' 1868, page 32), writes thus: "Gratiolet a eu entre les mains le cerveau d'un foetus de Gibbon, singe eminentement superieur, et tellement rapproche de l'orang, que des naturalistes tres-competents l'ont range parmi les anthropoides. M. Huxley, par exemple, n'hesite pas sur ce point. Eh bien, c'est sur le cerveau d'un foetus de Gibbon que Gratiolet a vu LES CIRCONVOLUTIONS DU LOBE TEMPORO-SPHENOIDAL DEJA DEVELOPPEES LORSQU'IL N'EXISTENT PAS ENCORE DE PLIS SUR LE LOBE FRONTAL. Il etait donc bien autorise a dire que, chez l'homme les circonvolutions apparaissent d'a en w, tandis que chez les singes elles se developpent d'w en a."), and the other of a human foetus at the 22nd or 23rd week of uterogestation, in which Gratiolet notes that the insula was uncovered, but that nevertheless "des incisures sement de lobe anterieur, une scissure peu profonde indique la separation du lobe occipital, tres-reduit, d'ailleurs des cette epoque. Le reste de la surface cerebrale est encore absolument lisse."

Three views of this brain are given in Plate II, figs. 1, 2, 3, of the work cited, shewing the upper, lateral and inferior views of the hemispheres, but not the inner view. It is worthy of note that the figure by no means bears out Gratiolet's description, inasmuch as the fissure (antero-temporal) on the posterior half of the face of the hemisphere is more marked than any of those vaguely indicated in the anterior half. If the figure is correct, it in no way justifies Gratiolet's conclusion: "Il y a donc entre ces cerveaux [those of a Callithrix and of a Gibbon] et celui du foetus humain une difference fondamentale. Chez celui-ci, longtemps avant que les plis temporaux apparaissent, les plis frontaux, ESSAYENT d'exister."

Since Gratiolet's time, however, the development of the gyri and sulci of the brain has been made the subject of renewed investigation by Schmidt, Bischoff, Pansch (78. 'Ueber die typische Anordnung der Furchen und Windungen auf den Grosshirn-Hemispharen des Menschen und der Affen,' 'Archiv fur Anthropologie,' iii. 1868.), and more particularly by Ecker (79. 'Zur Entwicklungs Geschichte der Furchen und Windungen der Grosshirn-Hemispharen im Foetus des Menschen.' 'Archiv fur Anthropologie,' iii. 1868.), whose work is not only the latest, but by far the most complete, memoir on the subject.

The final results of their inquiries may be summed up as follows:—

1. In the human foetus, the sylvian fissure is formed in the course of the third month of uterogestation. In this, and in the fourth month, the cerebral hemispheres are smooth and rounded (with the exception of the sylvian depression), and they project backwards far beyond the cerebellum.

2. The sulci, properly so called, begin to appear in the interval between the end of the fourth and the beginning of the sixth month of foetal life, but Ecker is careful to point out that, not only the time, but the order, of their appearance is subject to considerable individual variation. In no case, however, are either the frontal or the temporal sulci the earliest.

The first which appears, in fact, lies on the inner face of the hemisphere (whence doubtless Gratiolet, who does not seem to have examined that face in his foetus, overlooked it), and is either the internal perpendicular (occipito-parietal), or the calcarine sulcus, these two being close together and eventually running into one another. As a rule the occipito-parietal is the earlier of the two.

3. At the latter part of this period, another sulcus, the "postero-parietal," or "Fissure of Rolando" is developed, and it is followed, in the course of the sixth month, by the other principal sulci of the frontal, parietal, temporal and occipital lobes. There is, however, no clear evidence that one of these constantly appears before the other; and it is remarkable that, in the brain at the period described and figured by Ecker (loc. cit. pp. 212-213, Taf. II, figs. 1, 2, 3, 4), the antero-temporal sulcus (scissure parallele) so characteristic of the ape's brain, is as well, if not better developed than the fissure of Rolando, and is much more marked than the proper frontal sulci.

Taking the facts as they now stand, it appears to me that the order of the appearance of the sulci and gyri in the foetal human brain is in perfect harmony with the general doctrine of evolution, and with the view that man has been evolved from some ape-like form; though there can be no doubt that form was, in many respects, different from any member of the Primates now living.

Von Baer taught us, half a century ago, that, in the course of their development, allied

animals put on at first, the characters of the greater groups to which they belong, and, by degrees, assume those which restrict them within the limits of their family, genus, and species; and he proved, at the same time, that no developmental stage of a higher animal is precisely similar to the adult condition of any lower animal. It is quite correct to say that a frog passes through the condition of a fish, inasmuch as at one period of its life the tadpole has all the characters of a fish, and if it went no further, would have to be grouped among fishes. But it is equally true that a tadpole is very different from any known fish.

In like manner, the brain of a human foetus, at the fifth month, may correctly be said to be, not only the brain of an ape, but that of an Arctopithecine or marmoset-like ape; for its hemispheres, with their great posterior lobe, and with no sulci but the sylvian and the calcarine, present the characteristics found only in the group of the Arctopithecine Primates. But it is equally true, as Gratiolet remarks, that, in its widely open sylvian fissure, it differs from the brain of any actual marmoset. No doubt it would be much more similar to the brain of an advanced foetus of a marmoset. But we know nothing whatever of the development of the brain in the marmosets. In the Platyrrhini proper, the only observation with which I am acquainted is due to Pansch, who found in the brain of a foetal *Cebus Apella*, in addition to the sylvian fissure and the deep calcarine fissure, only a very shallow antero-temporal fissure (scissure parallele of Gratiolet).

Now this fact, taken together with the circumstance that the antero-temporal sulcus is present in such Platyrrhini as the *Saimiri*, which present mere traces of sulci on the anterior half of the exterior of the cerebral hemispheres, or none at all, undoubtedly, so far as it goes, affords fair evidence in favour of Gratiolet's hypothesis, that the posterior sulci appear before the anterior, in the brains of the Platyrrhini. But, it by no means follows, that the rule which may hold good for the Platyrrhini extends to the Catarrhini. We have no information whatever respecting the development of the brain in the Cynomorpha; and, as regards the Anthropomorpha, nothing but the account of the brain of the Gibbon, near birth, already referred to. At the present moment there is not a shadow of evidence to shew that the sulci of a chimpanzee's, or orang's, brain do not appear in the same order as a man's.

Gratiolet opens his preface with the aphorism: "Il est dangereux dans les sciences de conclure trop vite." I fear he must have forgotten this sound maxim by the time he had reached the discussion of the differences between men and apes, in the body of his work. No doubt, the excellent author of one of the most remarkable contributions to the just understanding of the mammalian brain which has ever been made, would have been the first to admit the insufficiency of his data had he lived to profit by the advance of inquiry. The misfortune is that his conclusions have been employed by persons incompetent to appreciate their foundation, as arguments in favour of obscurantism. (80. For example, M. l'Abbe Lecomte in his terrible pamphlet, 'Le Darwinisme et l'origine de l'Homme,' 1873.)

But it is important to remark that, whether Gratiolet was right or wrong in his hypothesis respecting the relative order of appearance of the temporal and frontal sulci, the fact remains; that before either temporal or frontal sulci, appear, the foetal brain of man presents characters which are found only in the lowest group of the Primates (leaving out the Lemurs); and that this is exactly what we should expect to be the case, if man has resulted from the gradual modification of the same form as that from which the other Primates have sprung.

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