Optical illusions of motion / by G. Stanley Hall.

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Bowditch, H. P. 1840-1911.
Hall, G. Stanley.
Ophthalmological Society of the United Kingdom. Library
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Publication/Creation

[London] : [Cambridge University Press], [1882]

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OPTICAL ILLUSIONS OF MOTION.

By H. P. BOWDITCH, M.D., *Professor of Physiology in the Harvard Medical School;* and by G. STANLEY HALL, Ph.D. Plate XVIII.

In 1834, R. Addam described in the *Philosophical Magazine* the fact, often before observed, that when, after looking at a sheet of falling water, the eyes were turned toward the adjacent bank, the latter with the rocks and trees upon it seemed for a short time to move slowly upward. This was explained by Addam and also by E. Javal by assuming that the eye followed the falling mass a moment, and then slipped back, and that this oscillation was associated with the impression of motion downward, but, by continuing after the eye had been turned upon a stationary object, caused us to attribute to the latter a movement in the opposite direction. This explanation is vague, was not favoured by the studies of nystagmus which it prompted, and has since been shown to be worthless, as we shall see later, by the fact that opposite motor after-effects are possible for the same retina at the same time.

Analogous observations were later made by Sir David Brewster in the early days of railroad travelling[1]. When, *e.g.*, after looking at objects from the window of a car we suddenly turn the eyes to the floor within, the latter seems to move away from our feet in the opposite direction. This apparent movement Helmholtz designates as dizziness (*schwindel*)[2], and explains it by saying that when the traveller tries to fixate the objects near the train outside, his eye must be moved rapidly in a direction opposite the motion of the train. After he has become accustomed to regard the volitional impulses thus put forth as adapted to the fixation of objects, he tries, unconsciously believing his eyes to be motionless, to fixate objects at rest in the same way; thus objects on the train seem to move in the opposite sense although they are relatively at rest. If, Helmholtz continues, instead of looking out of the car, a point on the window-pane be fixated, this optical dizziness does not occur, because no motion is made by the eyeball for the fixation of

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[1] See *British Association Reports*, 1845, '48, '61.

[2] *Physiologische Optik*, pp. 602-4.

objects, although those lying beyond the window-pane (and hence not accommodated for) are seen to flit past as before. Neither this nor the analogous experiment of Helmholtz upon the way in which opening and closing the eyes affects the apparent motion of objects after the cessation of a whirling movement of the body round its own axis is entirely in accordance with our observations. This hypothesis might explain the after-effects of any continuous or uniform motion in one direction, as, *e.g.*, when the drum of an ordinary kymograph suddenly stops; but the apparently opposite movement of a rotating disk when arrested, which Helmholtz thinks due to slight and probably circular movement of the eyeball following the movement of attention in the indirect field of vision, has led us to the opinion that modifications of muscular tension are but one of the less important factors in the explanation of this illusion. The phenomena of the rotating spiral which Helmholtz admits belongs to the same class of illusions, and especially the opposite after-effects of two spirals rotating in opposite directions at the same time and near together observed by us, seem conclusive against this theory.

More recently Dr. F. Guthrie, Aitken[1], and especially Professor Silvanus P. Thompson, have made valuable additions to our knowledge of these phenomena[2]. The apparent movement of the moon behind fast-flying clouds, the apparent backward motion of the water near the shores of a large river if the current is rapid at the middle, the apparent ducking forward of the masts of a ship in passing under a bridge from which it is observed, the seeming revolution of the landscape about any intermediate fixation point viewed from a moving train, the backward motion of stationary objects after viewing a procession,—these are a few of the more familiar forms of this class of illusions which Thompson proposes to call illusions of "subjective complementary motion" and to regard them as analogous to the more familiar phenomena of subjective complementary colours. His law is stated as follows: "The retina ceases to perceive as a motion a steady succession of images that pass over a particular region for a sufficient time to induce fatigue, and on a portion of the retina so affected the image of a body not in motion appears by contrast to be moving in a complementary direction." But the analogy between colours and motions in different directions in space is at best only remote and symbolic, so that the explanatory power of this law is

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[1] *Proceedings of the Royal Society of Edinburgh*, Nov., 1878.

[2] See articles by S. P. Thompson in *The Philosophical Magazine*, 1876, in *Quarterly Journal of Science*, March, 1879, in *Brain*, October, 1880.

extremely slight. Not only is the term "complementary" used with radically different connotations in the two cases, but Thompson is himself in doubt whether the phenomena he describes are after all subjective, or whether they may not be susceptible of a physical explanation. He says, "If the eye can alter at will the actual size of vertical images by double muscular adjustment between the magnifying power of the lenses of the eye and the distance of their equivalent optical centre from the surface of the retina"—this would "entirely cut away the significance of any crucial test with rotating spirals." Another objection to the so-called law is that in our experience the retina never ceases, nor tends to cease, to perceive motion as such.

Proceeding to the study of these phenomena, the illusion of the waterfall was readily reproduced by a belt five inches wide passing over two rollers 18 inches apart, one of which is turned by a crank. In front of this moving surface a flat wooden frame 16 inches wide is fastened and both belt and frame are striped horizontally in black and white as shown in Fig. 1. By turning the crank the centre of this striped surface receives a uniform movement, which seems to be reversed when it stops. This illusion is not impaired by the closest attention to the margin along which the lines of the belt happen to match or not with those of the frame. This scrutiny reveals of course in the clearest way that there is really no backward motion when the crank is arrested. We might expect that to accommodate this contradiction between sensation and judgment the lines would seem to bend out of their strictly horizontal direction, but they do not for an instant; yet the impression of backward movement persists inexpugnably.

In the second series of experiments a large pasteboard disk 22 inches in diameter was inscribed with a black spiral line three-quarters of an inch broad, with an equal interval of white, and making seven circuits before reaching the circumference. (See Fig. 2.) The effects of fixating this disk when in revolution are so striking with some observers as to cause great dizziness and even nausea, while all the curious after-effects described by Thompson and others are very manifest. If the revolution is in the direction in which the spiral line approaches the centre of the disk the entire surface of the latter seems to expand during revolution and to contract after it has ceased; and *vice versâ* if the movement of revolution is in the opposite direction. If in the former case the eyes of the observers are turned from the rotating disk towards any familiar object, *e.g.*, the face of a friend, the latter seems to contract or recede in a somewhat striking manner, and to expand or approach after the opposite motion of the spiral. We should expect that a straight line or a square hung before or fastened upon the disk so that each line passed across and projected beyond it would seem bent after or during the revolution. We should expect deflexion, especially where the image of the line left that part of the retinal surface occupied by the image of the disk, if not indeed where the retinal area of the two coincided. This, however, is not the case. In no case is such a line or square in the least deflected, although the illusions of contraction and expansion are unimpaired. The effect is perhaps best observed by transferring the gaze from the revolving spiral to a point upon a sheet of paper in the neighbourhood of a distinct black line. The surface of the paper seems to be animated with the contracting or expanding movement, while the line does not alter its direction in the least. Even for that part of the retina where the illusion is greatest the ability to judge of the straightness of lines is not sensibly affected. Even when lines pass across two spirals revolving in opposite directions, and giving rise to distinct and opposite after-effects, the eye being fixed upon a point between them, no deflexion whatever could be observed. The after-image of the revolving spiral if observed with closed eyes appears as a gray or yellowish circular tract in which the natural granulation of the field is more distinct than elsewhere on account of a peculiar boiling or seething sensation, which it is not easy to characterize further and from which alone it is not very easy to tell in which direction the spiral had revolved. This tract the line crosses without bending, and if the line is a broad one and is laid across the disk just before it has stopped revolving the boiling sensation can be realized on or through the after-image of the former.

Thus the same retinal elements stimulated at the same time give rise to the two opposite impressions of motion and rest. How this occurs we can only conjecture at present. Whatever may be the explanation of this phenomena the effect of the experiment is very striking, for the field of vision as a whole appears to be animated with a movement of contraction or expansion while the *separate points* in the field do not change their relative positions. The readiest assumption seems to be that the impression of motion either affects a different cerebral centre than that of the rest, or that one is more centralized or perceptive and the other more peripheral or more purely sensory. It is impossible to conceive how this persistent after-impression of motion can be a product of experience or association[1]. Experience cannot overcome nor volition reverse it as it may certain perspective figures. We cannot resist

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[1] See Helmholtz, *Physiologische Optik*, p. 438.

raising the question whether we may not be here very near attaining the *quale* of a real, pure sensation, not perhaps, as we might infer from Vierordt, itself motion, but only the more primitive element from which motor effects are inferred. Thompson conjectures that there may be "waves of nervous disturbance moving across the retina, one primary and in the same direction as the objective motion of the image upon the retina, the other secondary and later in time, giving rise to subjective motion of compensation." But nothing whatever is known of the constitution of the retinal elements which would enable them to produce illusions of aggregate motion in this or any other way. While therefore we readily admit that the general mental "form" suggested is that of elastic bodies or a disturbed fluid slowly regaining equilibrium, the inference that the seat of these illusions may be central rather than peripheral seems at present most natural. It should also be noted in passing that the edges of the broad black spiral lines appear to be quite jagged during rotation, as if the after-impression of their images were more persistent at some points of the retina than at others. The after expansions and contractions always seemed to us constant and gradual, and not intermittent or jerky as they appeared to Professor Thompson.

Another very different optical illusion of motion, described but not clearly explained by Thompson, is caused by giving to a series of concentric circles such as are often used to test astigmatism (see Fig. 3) a slight but rapid circular movement, by which every point of the figure without rotation is made to describe a circle of the same dimensions, and at a rate which may be indefinitely varied, four or five times round in a second being generally most effective. This movement is like that used in rinsing a circular dish half filled with water, and we will henceforth designate it, as Professor Thompson has proposed, as the "rinsing" movement. In order to study the phenomena thus caused, the following apparatus (shown in Fig. 4) was devised. Two inches in front of an upright plank, A, two feet in height, and ten inches broad, a wheel, B, six inches in diameter, was fastened so that it could be turned in a plane with the plank by a crank behind, or, by attaching a long belt, by the observer, ten feet in front. This central wheel turned two others, C, C, three inches in diameter, one on each side, by peripheral cogs. From the face of these smaller wheels projected pivots, D, D, which were so arranged that they could be adjusted at any distance from the centre of the wheels, less than half an inch. A strip of brass, with a hole in one end, played upon each of these pivots, a nut on the end of the pivot preventing them from falling off. The two strips of brass were screwed, one to each edge of a piece of thin board, E, eight inches square, which could thus be made to move in circles of varying dimensions corresponding to the excentricity of the pivots. Upon this board were fastened the cards displaying the figures which produced, when rotated as above described, the illusions of motion which were to be studied. Another board, E, of the same size, sliding in horizontal bearings, G G, could be connected by a crank movement with one of the pivots and thus used to impart to cards secured upon it a rapid horizontal movement to and fro.

When a chart upon which concentric circles are inscribed is rapidly shaken horizontally upon the vibrating table last described, the lines of the two opposite perpendicular sectors remain very distinct, while the lines upon the lateral sectors are blurred, or become quite gray if the movement is through a space equal to or greater than the width of the lines and is very rapid. This is due to the fact that so long as the movement is in the same direction as the white lines, as in the case of the perpendicular sectors, the same retinal elements are constantly stimulated, while if the movement is across them, as it is over the lateral sectors, alternating images of the dark and light lines follow each other in rapid succession across the same retinal surface. This fact is the key to the explanation of the phenomena caused by the same chart upon the other or rotating table when the circles seem to revolve. During every instant of the "rinsing" movement here, all lines in the same direction as the motion are distinctly seen, and all those at right angles to it are blurred. This explains the phenomena of alternate light and dark rotating sectors, and, in a large figure with many concentric circles the radius of most of which is very large compared with the excentricity of adjustment of the table, this is the chief cause of the illusion, which is distinctly observable if a dozen central circles are covered and only a few peripheral ones seen. At every instant all retinal impressions along one diameter are prolonged and intensified, while along another diameter at right angles to the first all impressions are shortened and obliterated, and the diameter on which these effects are observed, being shifted at each instant by the "rinsing" movement of the chart, produces the effect of rotating sectors.

But now it is plain that somewhere, near the centre of the entire figure of concentric circles, must be a circle some point in the circumference of which will always be presented to a fixed eye, because its radius is equal to that of the "rinsing" movement. This circle will, therefore, present the appearance of a circle revolving about a point in its circumference, as will be seen in Fig. 5. In this figure the circles drawn round the points A, B, C, D, represent four successive positions assumed by the system of concentric circles in consequence of the card on which they are drawn having the "rinsing" movement represented by the broken circle A, B, C, D, and it is evident that the optical effect is the same as if the entire system rotated about a point in the circumference of that circle, whose radius is equal to that of the "rinsing" circle (Circle 2 in Fig. 5), or in other words about a point in the centre of the "rinsing" movement[1]. This we readily demonstrated by rotating a figure representing a system of concentric circles round a slightly excentric point in the figure. In answer to the question why the latter movement never suggests the illusion of the former "rinsing" movement, we can only reply conjecturally, that we are probably more used from ordinary experience to associate all movements of circles with rotation so far as the phenomena will permit us to do so than with so unusual a movement of circles as that of "rinsing."

There remain only the residual phenomena of fainter, secondary, and often partial revolving rays or sectors which many eyes detect, for which we can only suggest the following possible explanation. If we contemplate the *star-test* for astigmatism, made of, *e.g.*, six straight lines crossing each other at equal angles in the centre, we shall observe, if we are astigmatic, that one or perhaps several of these lines will seem blacker or more distinctly drawn than the rest. If, instead of fixating the point of common intersection we accommodate for one of the primarily fainter lines, it, and perhaps others will in turn seem blacker and more distinct, and those that were formerly so will in turn appear fainter. Thus we may let an astigmatic eye circuit about such a figure fixating radius after radius, each transition bringing into greater distinctness not only the line fixated but certain other lines for which the lens in each position chances to have a homocentric focus. We have thus only to suppose that the astigmatic lens is slightly and perhaps unconsciously accommodated for the different positions of the primary light sectors above explained as they revolve, in order to account for the phenomena of the apparent rotation of the secondary ones. The form and number of the latter would of course vary with the astigmatic peculiarities in the form of individual lenses. These changes might be

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[1] Since writing the above we have observed a remark of Thompson's unnoticed before, that "the optical effect is equivalent to that of a ring excentric to an equal amount and actually rotating." The context of the remark, however, renders it doubtful whether its full bearing, as an explanation of the phenomena, was appreciated.

due to reflex modifications in the tension of the ciliary muscles, in which case the changes in the form of the lens would probably be too slight for the optometer to detect, and they and every modification in the direction of the attention might perhaps be quite independent of any movement of the eye-ball.

Finally it should be remarked that within wide limits the degree of illusion was found to be independent of the excentricity of the circular movement, and that no such proportionality as Professor Thompson conjectures was discernible between the latter and the width of the concentric circles.

The apparatus above described enables us moreover to analyze another very different class of phenomena also studied by Thompson. If, from a single strongly drawn circle a number of cogs project inward at equal intervals, the "rinsing" movement of the table causes an apparent slow movement of the circle in the opposite direction. This effect may be heightened by contrast if several such figures surround a system of concentric circles, as in Fig. 6, or *vice versâ* if one cogged circle is surrounded by several sets of concentric circles, as in Fig. 7. To be best seen the diameter of the "rinsing" circle should be *about* equal to the distance between the two adjacent cogs, although this admits of such very wide variations that it is impossible to lay down any rule. Beside the above circle with inward cogs another was drawn with cogs projecting outward, as in Fig. 8, when it was found that with the same movement of the table the two circles seemed to rotate in opposite directions—the latter rather more slowly. Parallel lines were then drawn with cogs projecting inwards, or from each toward the other at equal alternating intervals, as in Fig. 9. Upon giving this figure a "rinsing" movement the rows of cogs seemed to move off slowly in opposite horizontal directions. Even a circle composed of a series of unconnected dots was capable of giving rotatory effects, although less distinct than the cogs.

We will first take up the case of cogs projecting inward from two straight parallel horizontal lines (Fig. 9). Neither a vertical nor a horizontal movement would alone give rise to any illusion of motion, because the impression of motion in one direction would be directly cancelled by the impression of backward motion in the opposite direction. With the movement of rotation, however, parts of the contour of every figure would pass through a point of space and produce a retinal impression which could be repeated only by the same parts of the contour moving in the same direction in a subsequent revolution. The lower edge of the lower horizontal line would be seen when the "rinsing" table was at the point of its lowest depression moving, *e.g.*, to the right, and this retinal field would be confused by movements in no other direction. The movement of a straight line in the direction of its length, however, is not calculated to give a vivid motor effect. But when, after half a rotation the cogs, which project from the upper surface of the horizontal line, appear in a clear field moving off to the left, the motor effect, oft repeated, is vivid, for the points attract attention and concentrate and intensify the impression of motion. The backward motion of the cogs to their old position while the table is depressed is less distinctly perceived or realized, partly because they move through a portion of the field of vision partially obscured by after-images of other parts of the figure, and partly because the attention is constantly more occupied with those parts of the aggregate phenomenon not thus obscured, but where motor effects are more distinguishable and striking. This series of processes described for the lower line with upward cogs would, in Fig. 9, alternate with a corresponding series of movements in the opposite direction in the upper line with downward cogs.

If these horizontal lines were bent into semicircles, we should have, of course, the case of the wheel with inward cogs (Fig. 8A). Here we must hold fast to the same distinction between the area of confused after-images moving in different directions where specific effects are lost to consciousness, and the peripheral areas, through which the movement of projecting parts is always in the same sense, and to which attention is chiefly attracted, as we have pointed out above. Here too it is not easy to measure, even approximately, the rate of motion so purely illusory, and the inference of which is from so extremely complex sensuous impressions as in this case. The degree of illusion does not seem to be strictly proportionate to the rapidity of the actual motion. If it is slow, and the attention is concentrated upon a single point or cog, the illusion often vanishes from that point, while the points indirectly seen still seem to move despite the evident impossibility of such movement, without distortion of the figure. If the motion is rapid, so that there is no fixation point, and the attention is diffused over the whole figure, the innermost edge of the aggregate image often seems illusively to move more rapidly than the peripheral half, and independently of it. The general effect of motion is best secured in indirect vision, and sometimes is aided by improper accommodation. This form of the circle with inward cogs affords the most striking of all these illusions. The deception is more complete than in the previous case of parallel cogged lines, because the effect of no part of the "rinsing" movement is lost, but during each instant of it new cogs are coming into the clear field of vision within, and producing their motor effects, while with the horizontal lines the vertical movements are without effect, and again no doubt because a circle more readily suggests rotation from our ordinary experience than parallel lines suggest movement in their own direction. The cogs may be too few, and the distance between them so great compared with the diameter of the "rinsing" circle, that absolutely no rotatory effect is produced, or again they may be too numerous, and the effect greatly reduced. The explanation of the opposite movement of a circle with outward cogs is conversely analogous to the above explanation of the movement with inward cogs. Why, when the interval between the points of the cogs is the same in both cases, this movement with external should seem slower than that with internal cogs, it is not easy to see, especially as a circle with cogs projecting both ways always remains stationary, as if contradictory sensations or inferences from without and within the circle cancelled each other. But why then do we have under some circumstances a slow, *quasi* residual rotation if the circle is not drawn at all, and we use only a series of unconnected dots or cogs, arranged in a circular order, and not too far apart? A study of the movement of the cogs as related to that of the circle in the two cases throws little light upon the subject. That part of the path described by each cog-point that is free from the after-images caused by the "rinsing" revolution of the circle, is of course greater for outward than for inward cogs. This is because the former describe a curve with its convexity in the same direction as that of the circle from which they project, while for the latter some effect is always lost by radial motion (see Fig. 10). Thus when we reflect that this difference might be made to increase as the diameter of the "rinsing" circle approximated that of the circle upon which the cogs project, it would seem that such a combination of the variable elements of the experiment might easily be made, that the illusion with outward cogs would be greatest. This, however, is so far from being the case, that the circle with outward cogs often does not seem to rotate at all until the "rinsing" movement is so rapid that the secondary effect of rotation in the opposite direction, caused by movement of cogs through the blurred part of the field, as above described, is produced, when the illusion of two opposite rotations, one within the other, suddenly arises and, perhaps with a little slowing of the actual movement or a greater effort at fixation, as suddenly vanishes. On the other hand, if anything depended upon the amount of angular movement caused by each

Fig. 1.

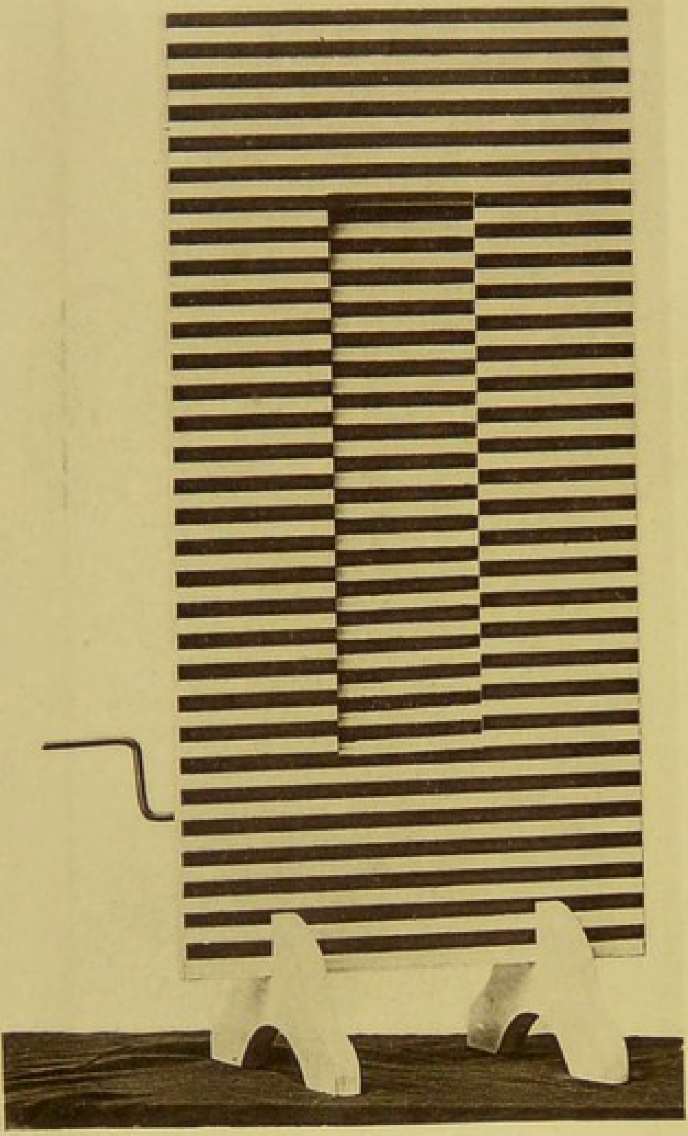


Fig. 2.

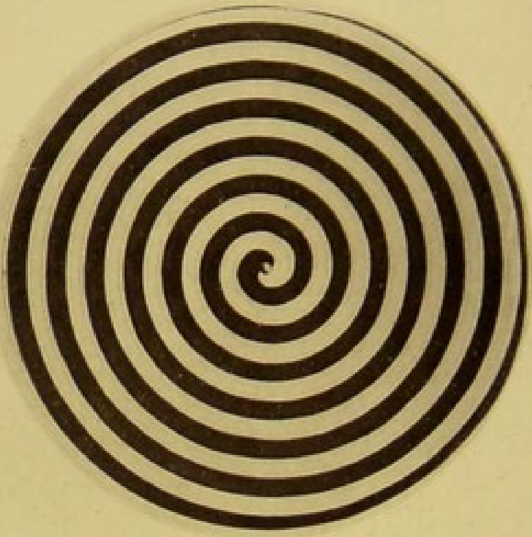


Fig. 3.

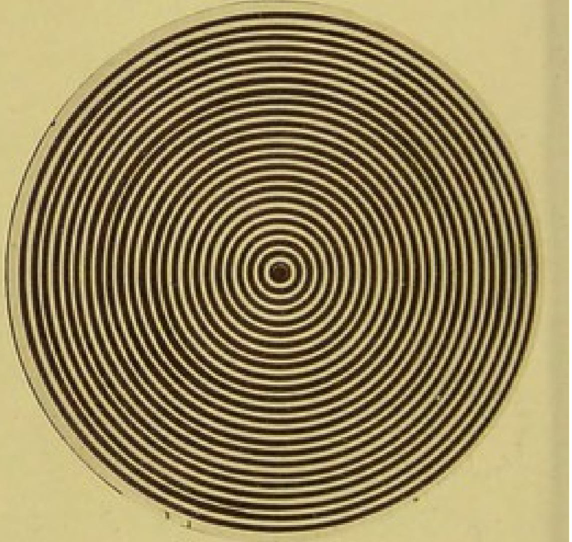
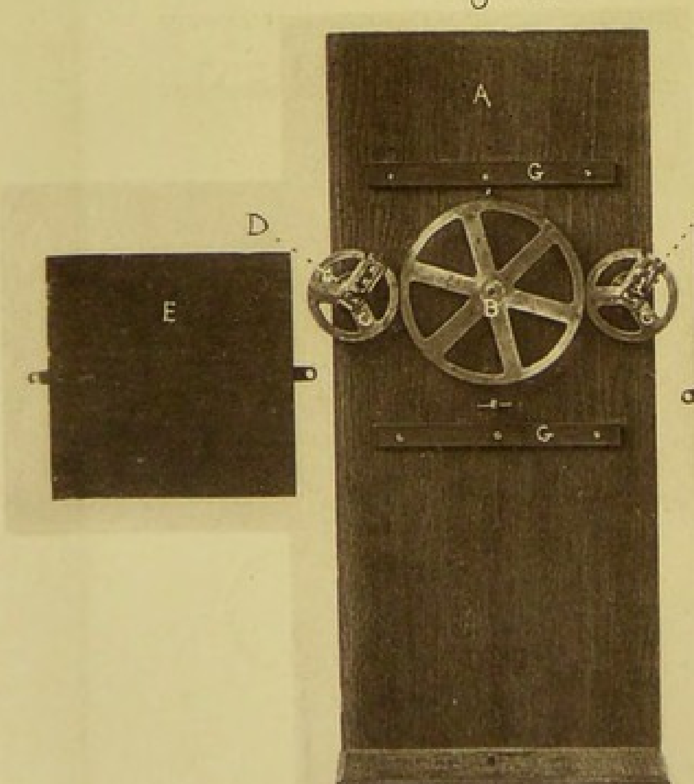


Fig. 4.



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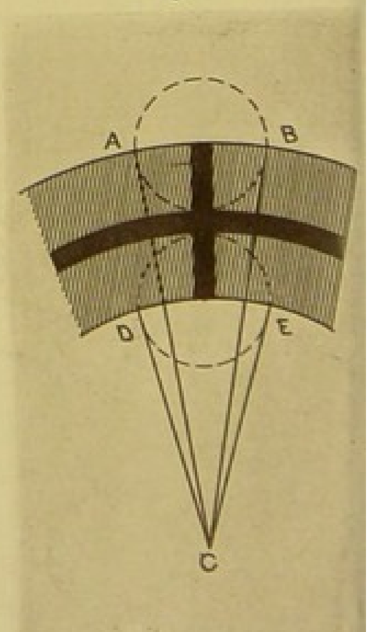
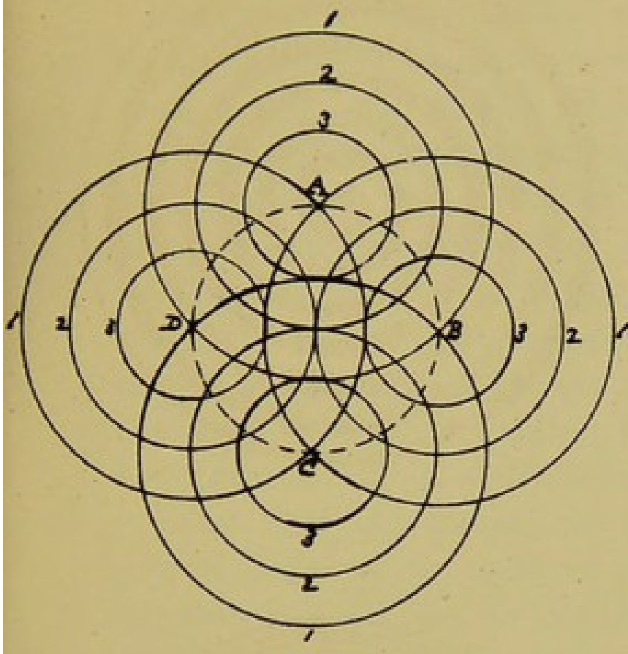


Fig. 5.



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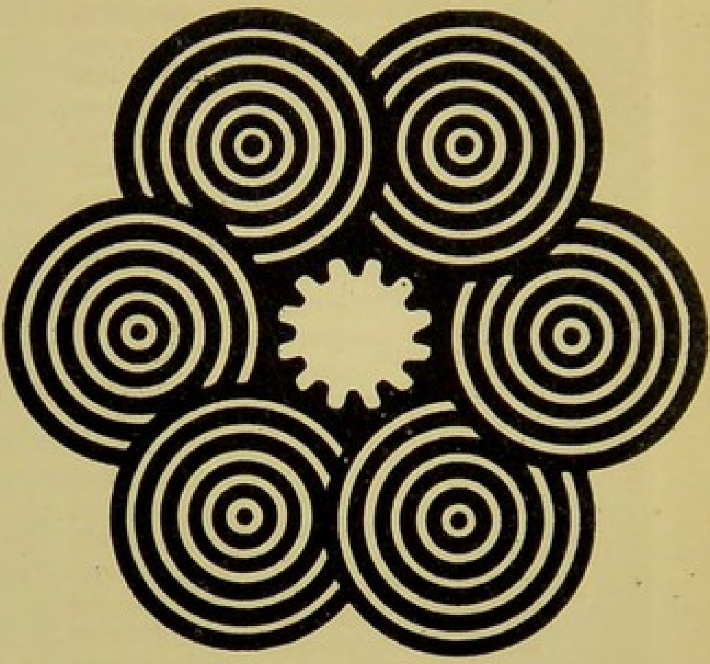

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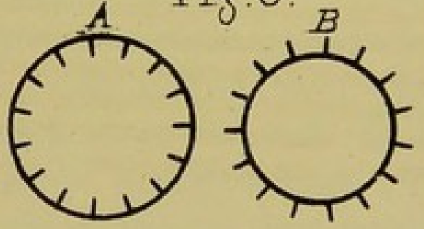


Fig. 6.

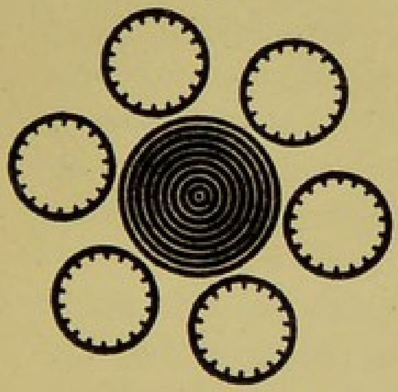


Fig. 9.

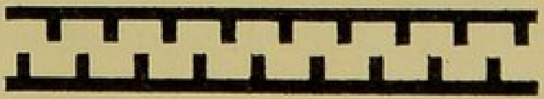
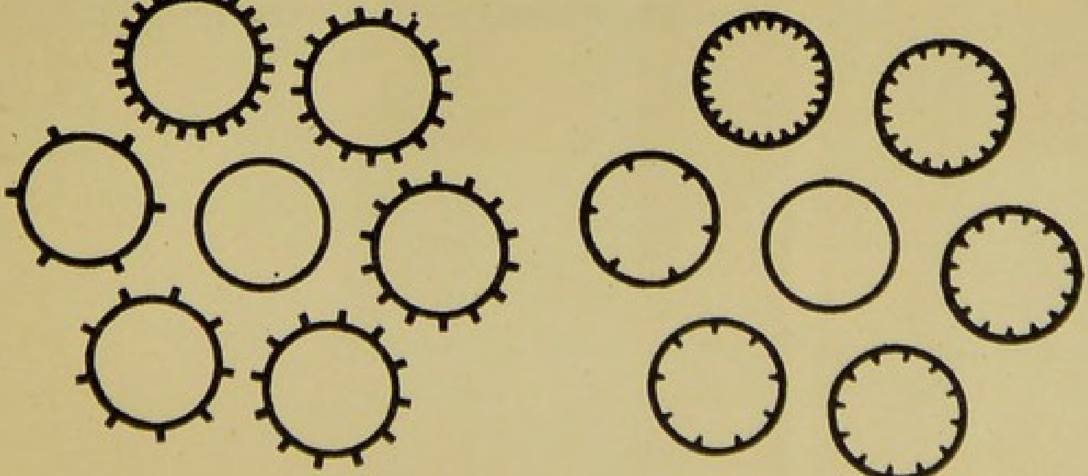


Fig. 11.



"rinsing" rotation, we should expect that with the dimensions compared by us, the illusion would be, as it is, less with outward cogs. These relations can be seen in Fig. 10, in which the small circles represent the space through which a single cog passes with each "rinsing" movement, and in which the unshaded part is unobscured by after-images. If the above supposition were really an explanation, then two adjacent circles of the same size as that of the figure, one with outward and the other with inward cogs, should seem to rotate with velocities which are related as the angles A C B and D C E respectively. That this is not the case may be seen by pinning two series of circles, as in Fig. 11, upon the "rinsing" table, with effects above described.

The only explanation we can propose is suggested by the very narrow limits of the field of most distinct vision[1]. Even for motor impulses it is not easy for the attention to be dispersed over a wide field, and it must especially be more natural for it to take in the sum total of effects from the inside of the entire figure, while many outside effects are lost to consciousness and all are probably enfeebled, than, conversely, to neglect the central contours and distribute itself around them. Even when turned upon a portion of the indirect field of vision, to do this would be—to speak paradoxically—to make its centre indirect. This explanation seems not improbable when we reflect that the very function of attention seems to be to exclude most of the many sensuous impressions we are continually receiving and to connect all others that are admitted to consciousness at a given moment, however dissimilar they may be, into a single complex concept[2]. It is true of attention as of vision, that the narrower and sharper its focus, the darker the rest of the field becomes; so that to neglect central shapes and processes in a circular figure and take in all its peripheral phenomena at the same moment would be as impossible for one as for the other.

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[1] See E. H. Weber, in Wagner's *Handwörterbuch*, Bd. IV., p. 532. See also pp. 558-9.

[2] See Hermann's *Handbuch der Physiologie*, Bd. II., Theil 2, p. 283; and Wundt's *Grundzüge der physiologisch. Psychologie*. Zweite Auflage, Bd. II., p. 207.

REFLEX MOVEMENTS OF THE FROG UNDER THE INFLUENCE OF STRYCHNIA.

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As long as animals in a normal condition were used for experiments upon reflex movement, it seemed probable that these movements were limited by fixed anatomical associations of reflex centres into groups which connected certain nerves of motion with certain nerves of sensation. Such an arrangement of cells and fibres in the central nervous system would explain the co-ordinated series of movements made to remove an irritation from a certain spot, as is seen on the application of a weak acid to the skin of the brainless frog. To explain the spread of the movements to new sets of muscles on increasing the irritation or the sensitiveness, one would need only to extend the hypothesis, and suppose these groups constituting the reflex apparatus to be connected in such a way that two or more could be brought into action at once without losing their several attributes.

This theory fails, however, to explain the appearance and extent of the reflex convulsions in an animal poisoned with strychnia. When a certain amount of this alkaloid has been absorbed, any stimulus, wherever applied, causes, as is well known, a spasm in all the muscles of the body, as if all the motor nerves were connected in the circuit of an induction coil. If then, during strychnia poisoning, every motor nerve in the body is capable of being called into activity by the stimulation of any sensory nerve, all these nerves must be freely connected in the spinal cord; for the strychnia certainly cannot bring about a change in the arrangement of fibres.

The small dose and short time required to produce strychnization lead to the supposition that a change takes place in the structure of

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THE

CONVOLUTIONS OF THE BRAIN:

A STUDY IN COMPARATIVE ANATOMY.

BEING AN

ADDRESS DELIVERED TO THE ANATOMICAL SECTION

OF THE

TENTH INTERNATIONAL MEDICAL CONGRESS IN BERLIN,
AUGUST 5, 1890.

BY

SIR WILLIAM TURNER, KNT.,
M.B., D.C.L., LL.D., F.R.SS. L. AND E.,
PROFESSOR OF ANATOMY IN THE UNIVERSITY OF EDINBURGH.

WITH NUMEROUS ILLUSTRATIONS IN TEXT.

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AND 20 SOUTH FREDERICK STREET, EDINBURGH.
1890.

THIS Address "On the Comparative Anatomy of the Convolutions of the Brain" was prepared at the request of the Committee of Organisation of the Anatomical Section of the Tenth International Medical Congress, which met in Berlin in August 1890. It was illustrated by a series of fifty large diagrams, most of which were made by Mr Herbert Goodchild from dissections prepared for the purpose, and the same gentleman has drawn carefully from nature, in pen and ink, a large proportion of the figures with which the Address, as now published, is illustrated. Figures 4, 5, 6, 8, 12, 14 and 16, which show the relations of the cerebrum and cerebellum to each other, and in which the corpora quadrigemina are completely concealed, were drawn before the brains were removed from the cranial cavity. I wish to thank my assistant, Mr James Simpson, for the efficient manner in which he exposed these brains within the skull.

THE

CONVOLUTIONS OF THE BRAIN:

A STUDY IN COMPARATIVE ANATOMY.

THE theme, "The Convolutions of the Brain," is one of profound interest to the physiologist, the psychologist, the pathologist, and the physician. But their respective studies of the functions and diseases of the cortex of the hemispheres cannot be satisfactorily conducted without the aid of the morphologist. So complex is the surface of the human brain that the signification of its various parts cannot be properly understood without constant reference to the appearance and arrangement of the surface of the hemispheres in other vertebrates, more especially the Mammalia.

The subject is one of so great an extent that I cannot do more in the limited time at my disposal than give a mere sketch of the arrangement of the grey cortex in specimens selected from different orders of mammals. Want of time will also prevent me from entering into a detailed analysis of the work of the numerous anatomists who have contributed to our present knowledge of the subject. I should wish, however, to pay my respectful tribute to the labours of Foville, Leuret, Gratiolet, Gervais, Broca and Beauregard, in France; of Rolando and Giacomini, in Italy; of Tiedemann, Burdach, Rudolph Wagner, Ecker, Bischoff, Pansch, Benedikt, Meynert and Krueg, in Germany; of Guldberg, in Norway; of Burt Wilder, in the United States; of Owen, Huxley, Flower, Rolleston, Marshall, Garrod, Ferrier and Cunningham, in Great Britain.

When the surface of a cerebral hemisphere is carefully examined, it is seen to be capable of a natural division into two parts: a basal region, or Rhinencephalon, and a superior portion, or Pallium. The demarcation between these two parts is due to the presence of a fissure, more or less distinctly defined in different animals, which has been named the *rhinal* or *ecto-rhinal* fissure. Our knowledge of this division is based upon the study of the development of the brain in different animals, as well as upon its comparative anatomy. It has been distinctly recognised by Owen and other anatomists. Broca wrote two admirable memoirs[1] on the subject, and laid especial stress on the modifications in the size of the rhinencephalon, or olfactory part of the brain, in the Mammalia. He has classified the Mammalia, in relation to the magnitude of their olfactory apparatus, into two groups: osmatic mammals, which possess a well-developed rhinencephalon with a keen sense of smell, and anosmatic mammals, in which the rhinencephalon and olfactory sense are either feeble or not developed at all. This classification is, however, logically defective, because in one and the same group are included both mammals which have the sense of smell, though it is not in them a dominant faculty, and mammals which are destitute of olfactory organs. I propose, therefore, to modify the classification of Broca, and to arrange the Mammalia in relation to the development of the olfactory apparatus into three groups:—

(*a*) Macrosmatic, where the organs of smell are largely developed, a condition which is found, for example, in the Ungulata, the proper Carnivora and indeed in the majority of mammals.

(*b*) Microsmatic, where the olfactory apparatus is relatively feeble, as in the Pinnipedia, the Whalebone Whales, Apes and Man.

(*c*) Anosmatic, where the organs of smell are apparently entirely absent, as in the Dolphins, and it may be in the Toothed Whales generally, though, as regards some genera of Odontoceti, we still require further information.

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[1] "Le grand lobe limbique et la scissure limbique," *Revue d'Anthropologie*, 1878; and "Recherches sur les centres olfactifs" *Revue d'Anthropologie*, 1879.

RHINENCEPHALON.

The separation of the rhinencephalon from the pallium or cerebrum proper by a rhinal fissure is fundamental, and is seen, even in the lowest vertebrates. In *Petromyzon,* for example, the division is distinct, and the rhinal or ectorhinal fissure is present.

Amongst the Mammalia the extent and depth of the rhinal fissure (r) varies materially. In a number of mammals, as *Echidna, Phalangista, Halmaturus, Macropus, Lepus, Cholœpus,* it extends continuously, near the lower boundary of the hemisphere, from its anterior to its posterior end, as a well-defined fissure. In *Talpa* it is shallow, and passes from before backwards for about two-thirds the antero-posterior diameter of the hemisphere. In *Arvicola, Pteropus* and *Cynonycteris,* it extends for scarcely one-third the distance. In *Dasypus* it is divided into short anterior and posterior segments, not continuous with each other, and a similar arrangement is to be seen in *Sciurus.* In the Carnivora and Ungulata, owing to the considerable development of the pallium, the tendency of the fissure is to pass from the lateral to the inferior surface of the hemisphere. In Apes and in Man, from the great reduction in size of the rhinencephalon, the rhinal fissure is limited to the region of the Sylvian fossa.

The rhinencephalon consists of an olfactory bulb, a crus or peduncle, and a lobus hippocampi, which vary in appearance,

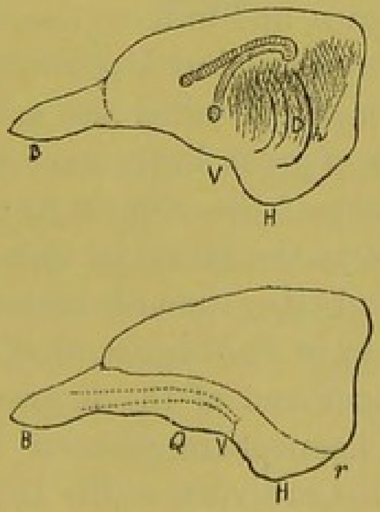

FIG. 1.—Hemisphere of macrosmatic Rabbit. The upper figure is the mesial surface, the lower the cranial surface.

position, and size in different mammals. In *Echidna* they present a grey surface, so that the lobus and crus look like a continuous convolution. Usually, however, white bands appear on the surface of the crus, which, in the Horse, Dog, and other macrosmatic mammals, are of considerable breadth. Even in such small brains as those of the Rabbit and Marmot slender white bands can be seen on the surface of the crus. In the human brain, and those of Apes, the surface of the crus is composed of white matter, similar in appearance to that of the external and internal roots of the olfactory peduncle.

The *bulbus* (B) is the most anterior part of the rhinencephalon. As its name expresses, it has a bulb-like swelling, and, except in Man and the higher Apes, projects forwards or upwards in front of the anterior end of the hemisphere.

The *crus* or *pedunculus* is, as a rule, separated from the bulbus by a constriction. In Man, Apes, Seals and Whalebone Whales it is slender and stalk-like. But in most mammals, as is well seen in the Ungulata, it is thick and band-like. Immediately in front of the area known in human anatomy as the *locus perforatus anticus*, but to which, in the comparative description of this part of the brain, the name of *quadrilateral space* (Q) is frequently applied, the olfactory peduncle divides into roots. Two of these are visible on the surface. They are called external and internal, and the external (*ex*), which is larger and more distinct than the internal (*in*), forms the outer boundary of the quadrilateral space, and in most mammals can be readily followed backwards into the lobus hippocampi.

The *lobus hippocampi* (H), called also natiform protuberance, or lobus pyriformis, is of great importance, for it is the central origin of the outer root of the olfactory peduncle. It forms a well-marked eminence in the brains of mammals generally. In the lower mammals, whether smooth-brained, as in *Lepus* and *Talpa*, or convoluted as in *Echidna* and *Macropus*, it is at the basal part of the hinder end of the hemisphere, and visible at the side when the hemisphere is seen in profile. In the Ungulata, and in such Carnivora as the Dog, it is best seen on the basal surface; for, owing to the development of the pallium backwards and downwards, it is no longer at the posterior end of the hemisphere, and is only partially seen on the lateral aspect. In the Walrus and Seals (fig. 2) the still greater development of the pallium has thrown it towards both the basal and the inner surface of the hemisphere. In Man and Apes, where it is known as the *uncus* or *unciform convolution*, it is entirely on the inner surface of the hemisphere, and is concealed both laterally and inferiorly by the enormous development of the temporo-sphenoidal lobe. Hence the lowest part of the hemisphere in this region is not formed by the same structure in all the Mammalia. In the more lowly organised brains the lobus hippocampi is the most depending part, but in the higher brains the convolutions of the temporo-sphenoidal lobe project downwards beyond it.

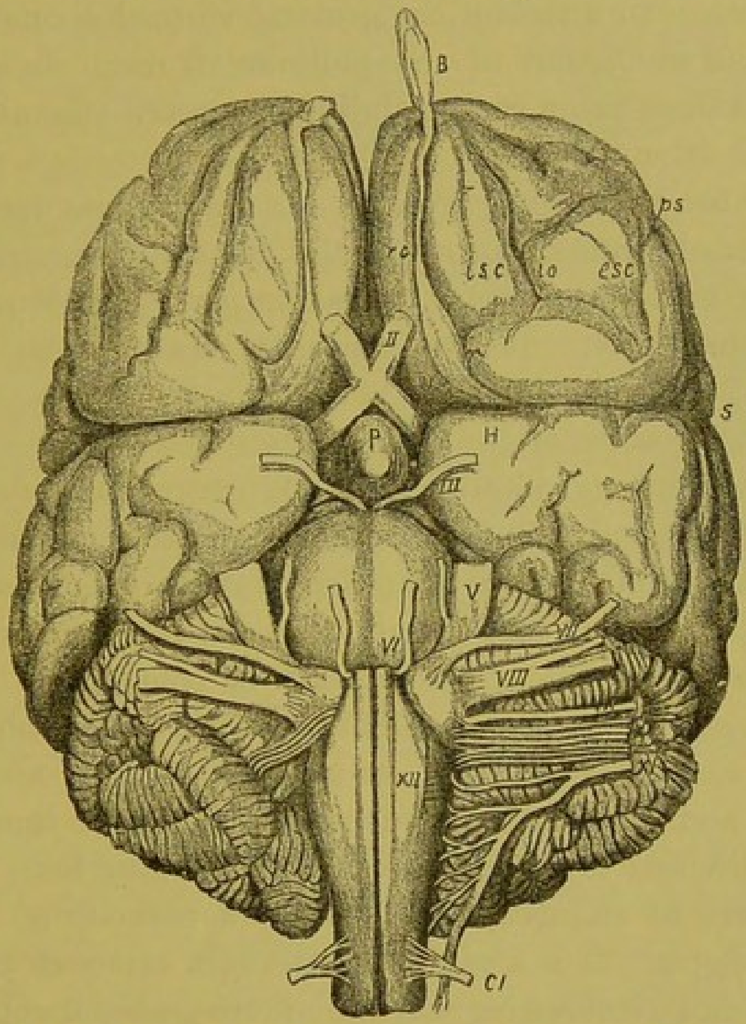

FIG. 2.—Basal surface of the brain of the microsmatic Elephant Seal (*Macrorhinus leoninus*).

Its size, in relation to that of the entire hemisphere, varies much in different mammals. In the smooth-brained Insectivora and Rodentia, for example, the lobus hippocampi forms a considerable proportion of the hemisphere. In an *Erinaceus europæus* (Hedgehog) its greatest vertical diameter was 7 mm., whilst that of the pallium was only 8 mm. In a *Talpa europæa* (Mole), their vertical diameters respectively were 3 and 6 mm. In a Rabbit the greatest vertical diameter of the lobus was 8 mm., that of the pallium 16 mm. In a Marmot (*Spermophilus*) their corresponding respective diameters were 7 mm. and 16 mm.

As the brain becomes convoluted, the pallium increases in size in a much greater ratio than the lobus hippocampi, until in the higher brains the lobus forms but a very small proportion of the hemisphere. This is especially seen in the brains of anthropoid Apes and Man.

The consideration of the size of the lobus hippocampi in the Cetacea is of especial interest, owing to the remarkably modified olfactory apparatus in those mammals. In the common Porpoise (*Phocæna communis*), in which the olfactory nerves are not developed, the lobus hippocampi is situated on the under and inner face of the hemisphere, and is continuous with the antero-inferior end of the gyrus hippocampi. The lobus in the specimen examined is 8 mm. in greatest breadth and 18 mm. in length, and the cornu Ammonis is fused with that surface, which is directed to the cavity of the descending horn.

The brain of the Narwhal (*Monodon monoceros*) is represented in fig. 3. It is a very characteristic cetacean brain, and illustrates in an interesting way the antero-posterior compression of the hemispheres, and the great increase in transverse diameter, as compared with the brains of non-cetacean mammals. The brain of the Narwhal is also anosmatic, the lobus hippocampi (LH) is a distinct mass on the under surface of the hemisphere immediately behind the inner end of the deep Sylvian fossa. It is divided into an inner and an outer part by a fissure extending obliquely on its under surface. Its greatest breadth is 19 mm., and its antero-posterior diameter is 31 mm. Both the gyrus hippocampi and cornu Ammonis are prolonged into it. A non-convoluted area, 35 mm. in breadth and 27 mm. in antero-posterior diameter, is situated in front, and to the inner side of the Sylvian fossa and optic tract. It is the perforated or quadrilateral space (Q), the *area desert* of Broca, and no vestige either of olfactory peduncle or roots can be seen in connection with it.[1]

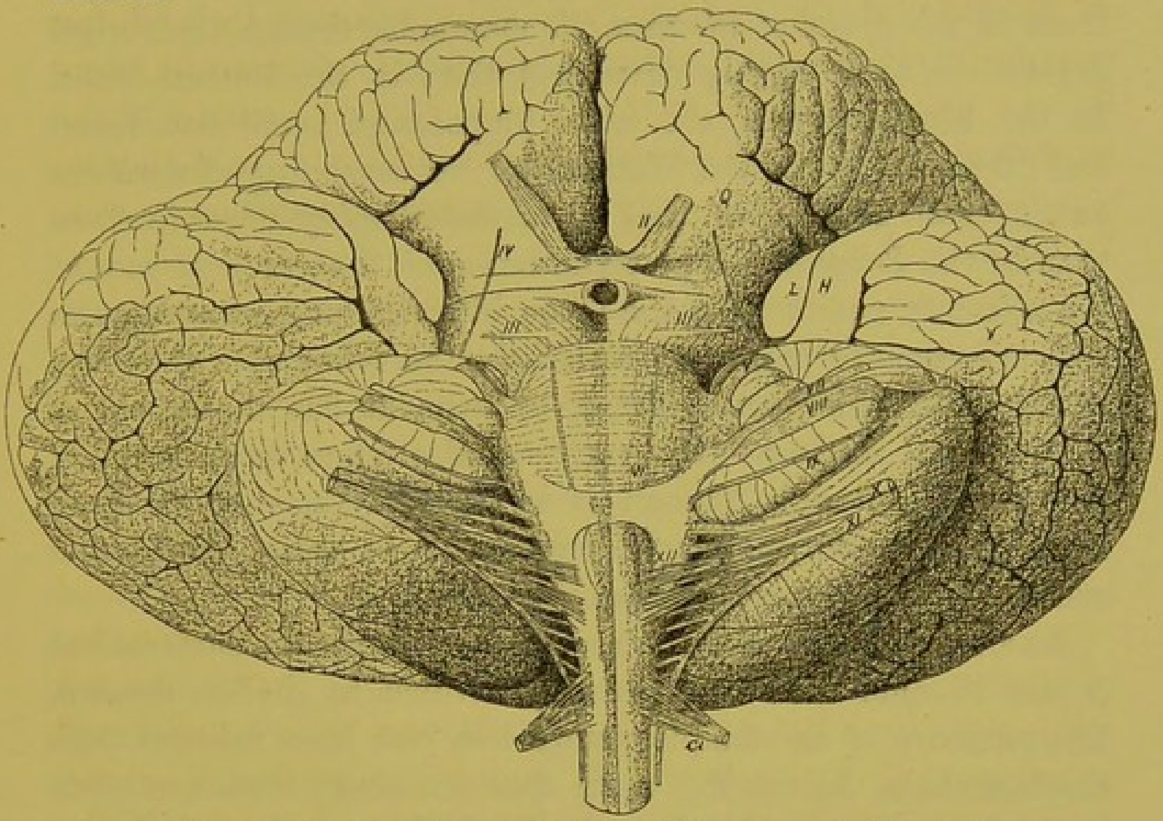

FIG. 3.—Basal surface of the brain of the anosmatic Narwhal (*Monodon monoceros*).

In a *Balænoptera rostrata* (fig. 33), where the olfactory peduncle and roots are small and rudimentary in relation to the size of the hemisphere, the lobus hippocampi is 32 mm. long and 18 mm. broad: its dimensions in relation to the size of the hemisphere being practically the same as in the Narwhal. The quadrilateral perforated area (Q) is also distinct, and bounded anteriorly by the inner and outer roots of the olfactory peduncle. Its transverse and antero-posterior diameters are respectively 25 mm.

The Porpoise, in the general dimensions of its cerebrum, approxi-

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[1] It is sometimes said that the reason why the Porpoise and other Delphinidæ have no olfactory organs is, because, from living in water, odorous particles would be so diffused and diluted that they could not excite the nerves of smell, which have accordingly atrophied and disappeared. But the Whalebone Whales, which have a similar habitat, have an olfactory apparatus, although it is small in relation to the size of the brain (fig. 33). Fish also have well-developed olfactory organs. The diffusion of odorous particles in an aqueous medium is not therefore a sufficient explanation of the disappearance of the smell apparatus in the Delphinidæ.

mates to that of the brain of the Elephant Seal, and the Walrus, animals in which the olfactory apparatus is of a size to include them in the group of microsmatic mammals, though their smell organs are more highly developed than in the human brain. In the Elephant Seal the lobus hippocampi is 19 mm. broad and 23 mm. long; in the Walrus the corresponding dimensions are 19 and 27 mm., so that it is considerably larger in them than in the Porpoise. The termination of the external root of the olfactory peduncle in the lobus hippocampi in macrosmatic and microsmatic mammals associates the lobus with the sense of smell, for which sense it is, as experiment has shown, one of the cerebral centres. The presence of a lobus hippocampi in anosmatic mammals, though it is relatively smaller in them than in osmatic mammals, leads one to infer that some additional function is to be associated with it.

As a rule, the lobus hippocampi is smooth on the surface, but it may in some brains be partially divided by shallow fissures. The presence of an oblique fissure has just been referred to in the Narwhal. In the Pig more than one short fissure extends in the long axis of the lobus; in the Ox a long fissure divides the lobus into an inner and an outer segment; one somewhat similar is seen in the Horse; whilst in the Polar Bear several curved furrows give its surface a convoluted appearance (figs. 3, 19, 26, 27).

The rhinal fissure separates the lobus externally, more or less perfectly, from the pallium, but the lobus also possesses a definite boundary, both internally and anteriorly.

The lobus is marked off internally by the *fissura hippocampi* (*h*), one of the fundamental fissures of the cerebrum (*grenz-furchen*). This fissure is visible on the inner and tentorial surface of the hemisphere, and forms at its lower end the inner limit of the lobus hippocampi. It curves upwards and forwards towards the splenium of the corpus callosum, but has not a constant mode of ending in that region. To take some examples: in the Pig, Ox, Horse, it ends below the splenium in the grey cortex of the convolution, which represents the upper end of the gyrus hippocampi; in many carnivorous animals it has a similar arrangement; in the Elephant Seal, Walrus, many Apes, and Man it turns round the splenium, and becomes continuous with the callosal fissure which bounds the corpus callosum superiorly; in *Dasypus sexcinctus* it ends in the posterior part of the callosal convolution; in *Echidna* and *Macropus* it curves upwards on to the mesial surface above the rudimentary corpus callosum.

The lobus is bounded anteriorly by a depression, which is named the *Vallecula,* or *Sylvian fossa* (v). This fossa varies materially in depth. In all macrosmatic brains it is shallow, and in some of these, as in *Talpa, Erinaceus, Lepus, Hyrax,* it is very faintly marked. Whenever the olfactory peduncle and its external root are large, the fossa is crossed in the antero-posterior direction by this root in its passage backwards to join the lobus hippocampi. In microsmatic and anosmatic brains, on the other hand, the fossa is considerably deeper. Two factors come into play in contributing to its depth. The one is an absolute and relative diminution in the magnitude of the rhinencephalon, which is accompanied by a constriction of the olfactory peduncle, and an imperfect development of its roots, more especially of the external root. The other is an absolute and relative increase in the size of the pallium in the region around the Sylvian fossa, so that the pallium is elevated and projects beyond it.

The Vallecula, or Sylvian fossa, belongs, therefore, fundamentally to the Rhinencephalon; though, in the process of evolution of the higher and more complex mammalian brains, the enormous development of the pallium in its immediate neighbourhood contributes materially to its depth, and it becomes continuous in them with the Sylvian fissure.

PALLIUM.

In all mammals the pallium is larger than the rhinencephalon, though the size is not so great proportionally in the lower as in the higher mammals. The pallium is the part of the hemisphere which, in a large number of mammals, possesses a more or less complex arrangement of convolutions. In some orders, however, the surface of the pallium is not convoluted, but retains throughout life the smooth appearance which is the universal characteristic of the cerebral hemispheres at an early stage of development. Even in some orders, where the majority of the species have convoluted brains, other species may retain the more primitive non-convoluted character. Mammals in whom the surface of the hemisphere is not convoluted are called smooth-brained, or Lissencephala.

The Insectivora are apparently the order in which the smooth-brained surface of the cerebral hemispheres is preserved throughout life most perfectly in all the genera.[1] I shall illustrate the appearance of the brain with figures of the British species, *Erinaceus europæus* (fig. 5) and *Talpa europæa* (fig. 4). The Rodentia also are almost universally smooth-brained (fig. 1). But in some genera traces of shallow fissures may occasionally be seen on the surface, which indicate an early stage in the formation of convolutions. Leuret and Broca figure a short, shallow, antero-posterior fissure on the upper part of the hemisphere of the Beaver (*Castor fiber*), a little to the outer side of the mesial longitudinal fissure, and the latter also figures a corresponding fissure in the Marmot and Rabbit. Leuret depicts a similar fissure in the Agouti. Broca figures a short antero-posterior fissure on the mesial surface of the pallium above the corpus callosum in the Beaver, Marmot, and Rabbit, which he names the limbic (splenial) fissure.[2] In *Cœlogenys paca* the pallium exhibits additional shallow fissures, which give it a still more convoluted character.[3]

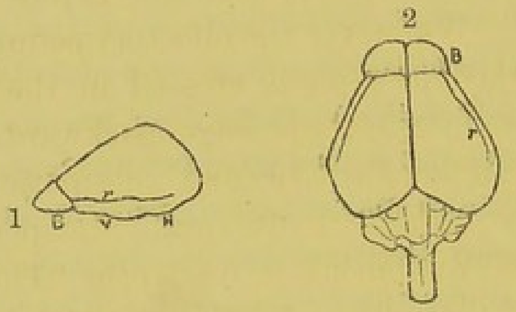

Fig. 4.—Brain of the Mole. 1, profile of hemisphere; 2, vertex view of brain.

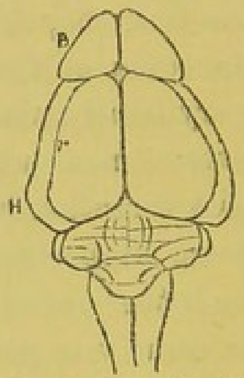

Fig. 5.—Vertex view of brain of Hedgehog.

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[1] Peters has described the brains of the Insectivorous genera *Solenodon*, *Rhynchocyon*, *Petrodromus*, and *Macroscelides*, in *Abh. der k. Akad. der Wiss.*, Berlin, 1863, and *Reise nach Mossambique*, 1852. A. H. Garrod has figured and described the brain of *Tupaia belangeri* in *Proc. Zool. Soc.*, 1879, and in Collected Scientific Papers.

[2] Rogner figures in *Zeitsch. f. Wiss. Zool.*, vol. 39, pl. xxxv. fig. 12, the brain of a Hare in which there is a splenial fissure.

[3] See Leuret, *Anat. Comp. du systéme nerveux*, pl. iii.

The Cheiroptera are usually regarded as smooth-brained mammals. This may probably be the case in the smallest Bats, but it does not apply to some of the larger species. Thus, in a Collared Fruit Bat (*Cynonycteris collaris*) a short sagittal fissure is situated in each hemisphere, a little external to the mesial longitudinal fissure, so as imperfectly to mark off a sagittal convolution forming the margin of the hemisphere. The sagittal fissure is better marked than in the brains of the Rabbit and Marmot. On the mesial surface of the same brain an antero-posterior fissure, corresponding to the limbic fissure of Broca—the splenial fissure of Krueg—divides the surface into callosal and marginal convolutions. The splenial fissure extends behind the splenial end of the corpus callosum on to the tentorial surface of the hemisphere, and differentiates the upper end of the gyrus hippocampi. In a *Pteropus medius* a fairly deep depression extends antero-posteriorly for nearly 4 mm. on the cranial surface about midway between the mesial longitudinal fissure and the lobus hippocampi. On the mesial face of the hemisphere a very

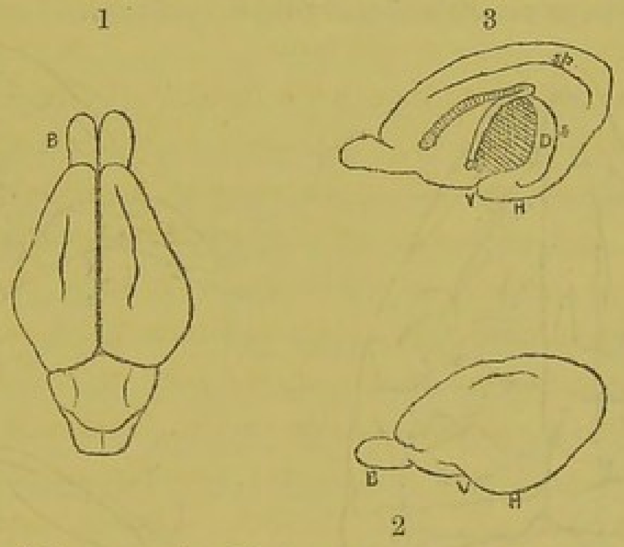

Fig. 6.—Brain of *Cynonycteris collaris.* 1, vertex view; 2, cranial surface; 3, mesial surface.

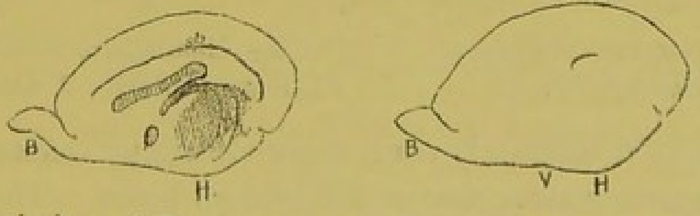

Fig. 7.—Hemisphere of *Pteropus medius.* 1, cranial aspect; 2, mesial surface.

distinct splenial fissure begins in front of the anterior end of the corpus callosum, and extends back to the tentorial surface, so that marginal, callosal and hippocampal gyri are all differentiated.

Other orders of mammals also contain species with both smooth and convoluted brains. Thus, in the Monotremata, *Ornithorhynchus* is smooth-brained. In each hemisphere the two fundamental limiting fissures (*grenz-furchen*), named rhinal (*r*) and hippocampal (*h*), which form the limits of the rhinencephalon, are present. In the concavity of the hippocampal fissure a distinct gyrus dentatus is situated. The surface of the pallium itself is, however, smooth, though I have seen it indented with shallow vascular furrows.

Echidna, on the other hand, has a convoluted brain. The species which I have examined is *E. hystrix*. The rhinencephalon with its fundamental limiting fissures (*r*, *h*) is distinct, and the gyrus dentatus is even more strongly denticulated than the corresponding structure in the human brain. The pallium is definitely convoluted, and measures 39 mm. in antero-posterior and 28 mm. in vertical diameter, but the fissures and convolutions on opposite sides are not symmetrical. Three fissures, 1, 2, 3,

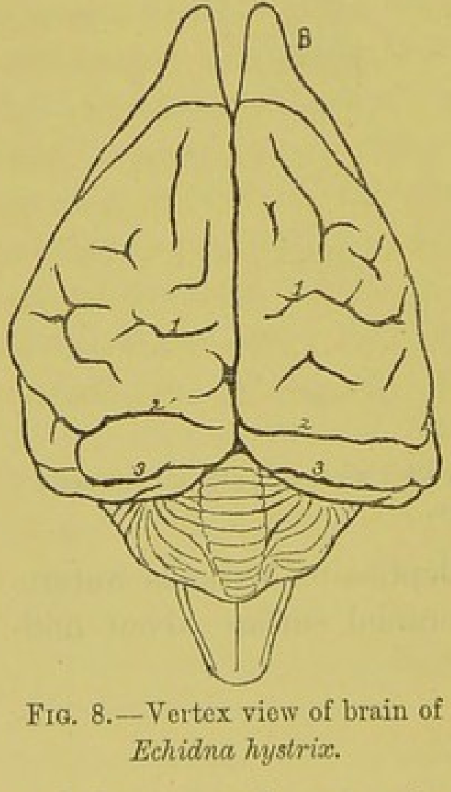

Fig. 8.—Vertex view of brain of *Echidna hystrix*.

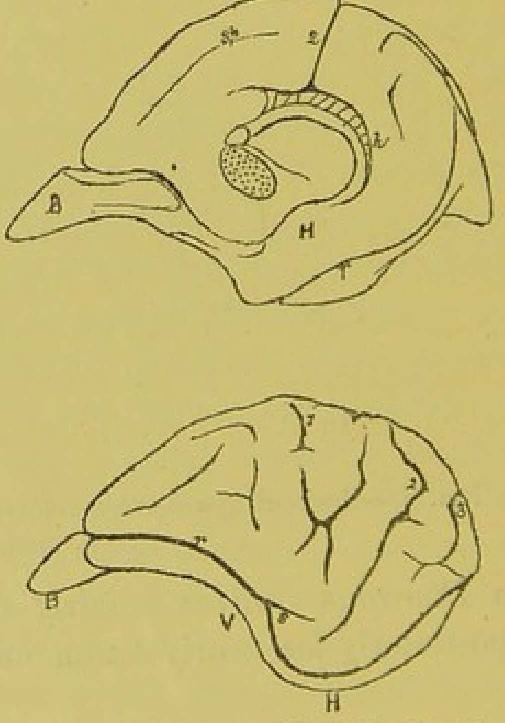

Fig. 9.—Hemisphere of *Echidna hystrix*. 1, cranial surface ; 2, mesial surface.

extend more or less completely down its outer surface in the vertical transverse or coronal direction, almost from the mesial longitudinal to the rhinal fissure, so as to map out convolutions having a similar direction, and these fissures have short subordinate fissures proceeding from them. The surface of the pallium in front of the most anterior vertical transverse fissure, No. 1, forms the anterior half of the pallium, and is divided by short antero-posterior fissures into small convolutions, the most posterior of which bounds No. 1 anteriorly. Vertical transverse fissure No. 2 in the right hemisphere turns round its upper margin, and becomes continuous with the fissura hippocampi. The vertical transverse convolution between the fissures Nos. 1 and 2 is partially divided into anterior and posterior limbs by subordinate fissures. A small fissure, marked *s* in fig. 9, may perhaps represent the Sylvian fissure. The mesial surface of the hemisphere possesses an antero-posterior fissure, which, although the corpus callosum is rudimentary, should be regarded as a splenial fissure. It divides this surface into two longitudinal convolutions, which are homologous with the callosal and marginal convolutions in the higher brains.

The Marsupialia also are in part smooth-brained and in part convoluted. In *Phalangista vulpina* rhinal and hippocampal fissures differentiate the rhinencephalon, and a shallow Sylvian fossa bounds the lobus hippocampi anteriorly. The cranial surface of the pallium is smooth, though two slight indentations at the margin of the hemisphere mark the beginning of two fissures, which traverse in the vertical transverse direction the mesial surface of the hemisphere. The more posterior of these two fissures extends to the tentorial surface of the hemisphere, and partially differentiates a gyrus hippocampi behind the hippocampal fissure, whilst in front of the last-named fissure is a

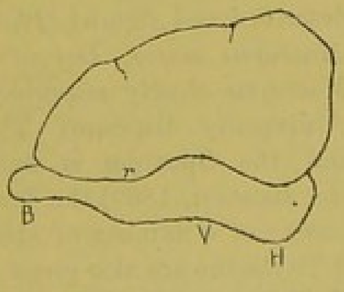

FIG. 10.—Cranial surface of brain of *Phalangista vulpina*.

distinct gyrus dentatus. A faint indication of a splenial fissure is above the rudimentary corpus callosum.

Dasyurus ursinus has also a distinct rhinencephalon, and the cranial surface of the pallium is smooth, though, as in *Phalangista*, also marked by shallow vascular furrows.[1] In *Halmaturus ruficollis* the limiting fissures of the rhinencephalon are distinct. The cranial surface of the pallium is traversed by three vertical transverse fissures, which radiate upwards from the rhinal fissure, and give a convoluted character to the surface.

In *Macropus major* the pallium is distinctly separated from the rhinencephalon. The cranial surface of the pallium is traversed by three fissures radiating upwards in the vertical transverse direction, and starting from the rhinal fissure immediately opposite the Sylvian fossa. The most anterior

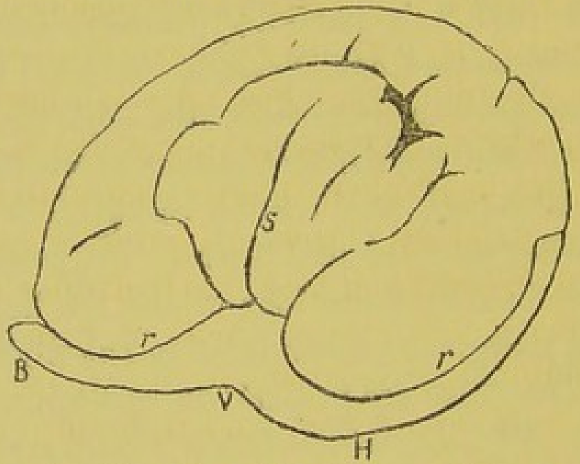

FIG. 11.—Cranial surface of hemisphere of *Macropus major.*

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[1] Sir Richard Owen has described and figured (*Phil. Trans.*, 1837) the brains of *Phascolomys wombatus*, *Macropus major*, *Dasyurus ursinus*, and *Didelphys virginiana*. The brain of Macropus closely resembles that figured above from a specimen in the Oxford University Museum. The Wombat is apparently more feebly convoluted, and the Opossum is smooth-brained. M. Gervais figures (*Nouvelles Archives du Muséum*, 1869) the brains of *Macropus giganteus* and the casts of the cranial cavity of a number of other marsupials. Figures of the Wombat, Kangaroo, and Thylacine are also given by Mr Flower in the *Phil. Trans.*, 1865. Mr W. A. Forbes figures and describes the brain of the Koala (*Phascolarctos cinereus*) in *Proc. Zool. Soc.*, 1881, and in Collected Scientific Papers, p. 183. The pallium is smooth, and is separated from the rhinencephalon by a rhinal fissure. The lobus hippocampi has a well-marked fossa Sylvii for its anterior boundary. A slight indentation in the pallium opposite the Sylvian fossa probably represents a rudimentary Sylvian fissure. The fissura hippocampi is distinct and prolonged on to the mesial face of the hemisphere above the small corpus callosum, and behind it is an *f*-shaped sulcus which reaches the upper and lower margin of the hemisphere.

radiating fissure is continued into an arcuate fissure which arches backwards above the middle radiating fissure, and almost reaches the posterior radiating fissure. The middle radiating fissure is apparently a Sylvian fissure (which is probably also the case with the corresponding fissure in *Halmaturus*). The convolution between it and the arcuate fissure is the convolution of the Sylvian fissure, and that between the arcuate fissure and the median longitudinal fissure is a marginal convolution. Behind the posterior radiating fissure a short vertical transverse fissure, not reaching the rhinal fissure, divides the part of pallium lying immediately above the lobus hippocampi into two convolutions.[1] The mesial surface, in addition to the fissura hippocampi, possesses a splenial fissure and callosal and marginal convolutions. The brain of a smaller species of *Macropus* in the University Museum[2] has only two fissures radiating from a spot in the rhinal fissure opposite the Sylvian fossa; the more posterior reaches the hinder end of the cerebrum, and is almost continuous with a fissure on the tentorial surface, which imperfectly differentiates the posterior boundary of a gyrus hippocampi situated behind the hippocampal fissure. A fissure, which may be called genual, is present on the anterior part of the mesial surface in front of and above the rudimentary corpus callosum (fig 12).

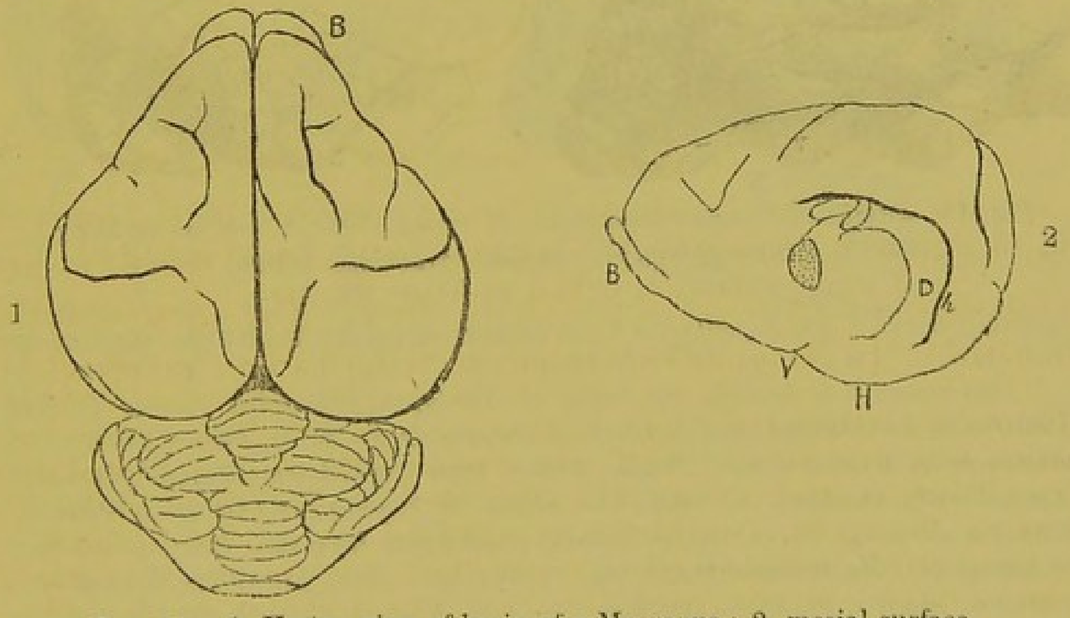

FIG. 12.—1, Vertex view of brain of a Macropus; 2, mesial surface.

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[1] This fissure has unfortunately been omitted by the draughtsman in figure 11.

[2] It is labelled "Bush Kangaroo."

The Edentata possess convoluted brains. The species which I have dissected are *Dasypus sexcinctus* and *Cholœpus hoffmanni*.[1] In *Dasypus*[2] an antero-posterior fissure traverses

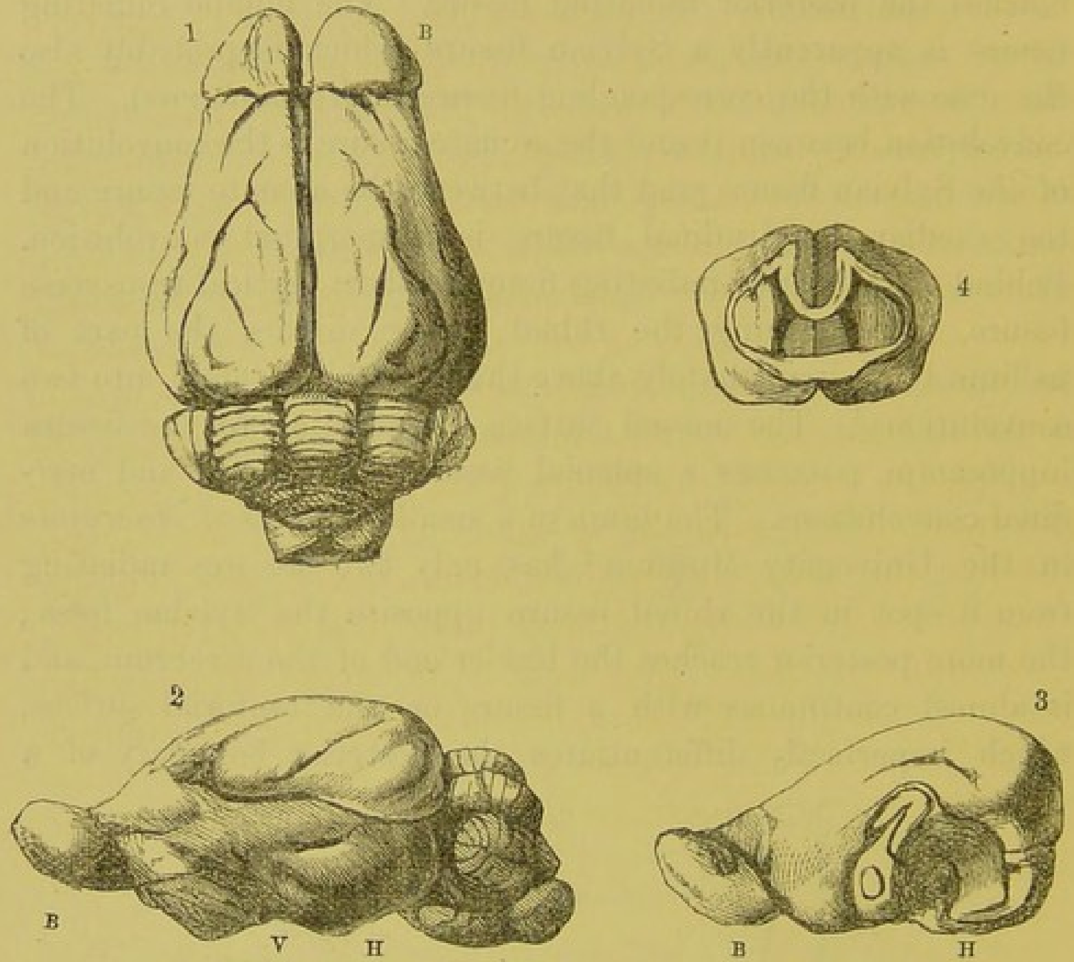

Fig. 13.—Brain of *Dasypus sexcintus*. 1, vertex view; 2, cranial surface; 3, mesial surface; 4, vertical transverse section.

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[1] Tiedemann has figured the brain of *Bradypus didactylus* (*Icones Cerebri Simiarum*, &c.); Rapp has described *D. novemcinctus*; W. H. Flower has figured *Cholœpus didactylus* (*Phil. Trans.*, 1865), Paul Gervais has figured (*Nouvelles Archives du Muséum*, v., 1869) the brains of *Euphractus* (*Dasypus*) *villosus*, *Manis temmincki*, *Myrmecophaga jubata*, *Orycteropus capensis*; Georges Pouchet (*Journal de l'Anat. and Phys.*, vols. v. vi., n.s., 1868, 1869) has figured the brains of Dionyx, Pangolin, and Bradypus; W. A. Forbes has figured the brain of *Myrmecophaga jubata* (*Proc. Zool. Soc.*, 1882, and in Collected Scientific Papers). In all these Edentates, except Dionyx, the pallium is convoluted, although the convolutions are more numerous in Myrmecophaga and Manis than in Dasypus. In Manis there is apparently, from Gervais's figure, a well-marked Sylvian fissure, and the fissure depicted by Forbes, *l.s.s.*, fig. 3, in Myrmecophaga is doubtless also the fissure of Sylvius.

[2] Fig. 13 is reproduced from my paper on the brain of *Dasypus sexcinctus* in *Jour. Anat. and Phys.*, vol. i. p. 314, 1867.

almost the whole length of the pallium, and turns round the posterior end of the hemisphere to become continuous with the hippocampal fissure. Two longitudinal convolutions are thus differentiated,—the one between this fissure and the interrupted rhinal fissure, the other between this fissure and the mesial longitudinal fissure,—and this latter convolution has a subordinate fissure in it. A short splenial fissure on the mesial surface marks off a marginal from a callosal convolution. In *Cholœpus,* near the anterior end of the pallium, a vertical transverse fissure extends upwards from the rhinal fissure, and turns round the upper margin of the hemisphere to the mesial surface; it marks off the anterior end of the pallium as a distinct convolution (fig. 14). Behind this fissure a longitudinal fissure extends backwards, which separates a marginal sagittal convolution bounding the mesial longitudinal fissure from a second longitudinal convolution situated lower down on the cranial surface of the pallium. Below this again is an arched fissure, which forms the upper limit of a third convolution, the lower boundary of which is the rhinal fissure. There is no definite Sylvian fissure, but a faint indentation in the lower border of the pallium, a little above the Sylvian fossa, may possibly be its representative. On the mesial surface of the pallium a splenial

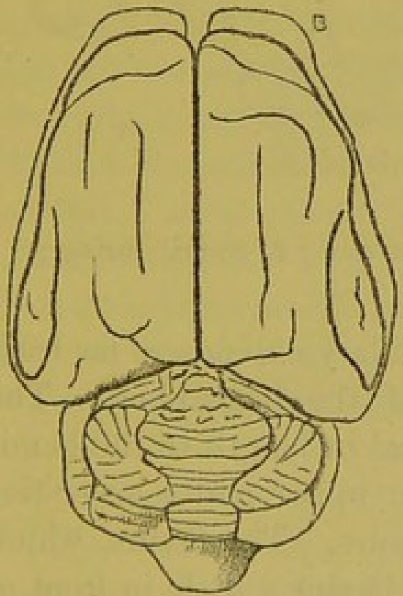

FIG. 14.—Vertex view of brain of *Cholœpus hoffmanni.*

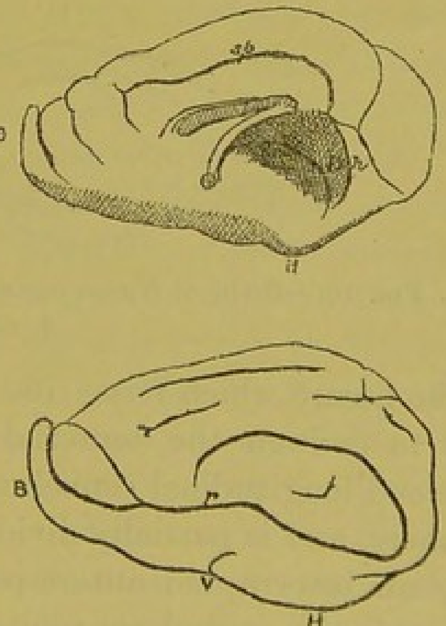

FIG. 15.—1, cranial surface; 2, mesial surface of hemisphere of *Cholœpus hoffmanni.*

fissure commences in front of the corpus callosum. It extends backwards to behind the splenium, and apparently becomes continuous with the hippocampal fissure. The convolution which forms the posterior boundary of the hippocampal fissure is bounded behind by a deep fissure, which below almost joins the posterior end of the rhinal fissure, whilst above it turns on to the cranial surface of the pallium and ends in the second longitudinal convolution, which it assists in partially dividing into an upper and a lower tier (fig. 15).

In *Hyrax*, also, the brain is convoluted. In *H. capensis* the cranial surface of the pallium is divided into tiers of longitudinal convolutions by antero-posterior fissures. The highest convolution is slender and almost equal in length to the hemisphere, and forms the margin (*m*) of the mesial longitudinal fissure. The fissure which forms its lower boundary extends so far back as to end on the tentorial surface of the hemisphere. The second longitudinal convolution is equal in length to the hemisphere, and is partially divided into an upper and a lower tier by an interrupted antero-posterior fissure. The fissure, which bounds the second convolution below, begins a little in front of the Sylvian fossa, and extends upwards and backwards almost to the hinder end of the hemisphere. Between this fissure and the rhinal is a relatively broad portion of the pallium, which is divided by two short vertical transverse fissures into three small vertical convolutions. The more anterior of these fissures has in

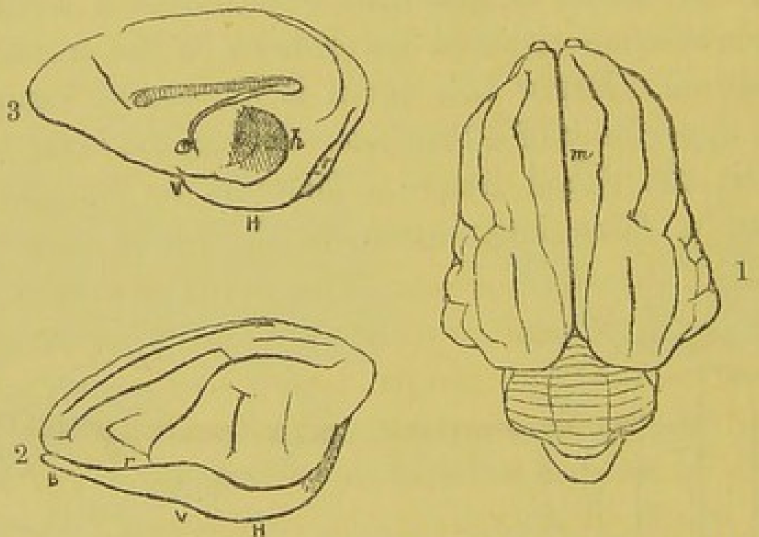

FIG. 16.—Brain of *Hyrax capensis*. 1, vertex view; 2, cranial surface; 3, mesial surface.

some respects the position and direction of a Sylvian fissure, but it scarcely reaches the rhinal fissure. The mesial surface of the hemisphere does not possess a splenial fissure, so that a callosal convolution is not demarcated from the marginal convolution; but a short vertical transverse fissure, which perhaps represents the *genual fissure* of Krueg, as seen in some of the Ungulata, is situated a little in front of the genu of the corpus callosum.

Before I pass to the consideration of the convolutions in those orders in which the pallium is elaborately convoluted, it may be of interest briefly to review the fissures and convolutions in the mammals just described, with the view of noting their order of relative appearance.

The importance of the rhinal and hippocampal fissures as fundamental limiting fissures for the rhinencephalon has already been referred to. But the fissura hippocampi (*h*) is also the limiting fissure for the gyrus dentatus (D), which is thus a fundamental gyrus, and is present in all mammals. Although in the brains of mammals so far apart as *Echidna* and *Homo*, the grey matter of this gyrus has the denticulated appearance which has led to its special descriptive name, yet in most mammals it is smooth on the surface. The gyrus dentatus varies in breadth. In the human brain it is a narrow stripe, and lies at the bottom of the hippocampal fissure, so that it is not easily seen until the tænia hippocampi is drawn on one side. In Mammalia, generally, it forms a distinct band visible on the surface. In the small brain of the Hedgehog (*Erinaceus*) it is 3 mm. broad, and in the very much larger brain of the Horse it is 6 mm. broad, so that it does not increase in size in the same ratio as the pallium. It is precisely bounded in front by the so-called transverse fissure of the cerebrum, through which the choroid plexus of the pia mater is projected towards the descending horn of the lateral ventricle. At its lower end it is fused with the lobus hippocampi of the rhinencephalon, and it is in relation with the projection into the descending horn called hippocampus major or cornu Ammonis.

Another fissure, which appears low down in the mammalian brain, is that which extends on the upper part of the cranial surface in the longitudinal or sagittal direction, parallel to the mesial longitudinal fissure; it marks off a convolution which may be called sagittal or marginal (*m*), for it forms the margin of the great mesial fissure. This fissure is, as previously stated, occasionally present in the brains of rodents and bats, and appears indeed in the pallium of these and some other mammals before there is any definite evidence of a Sylvian fissure.

In the study of the Sylvian fissure care should be taken to discriminate between it and the Sylvian fossa or vallecula. As already pointed out, the Sylvian fossa (V) is a depression in the rhinencephalon immediately in front of the lobus hippocampi, and it is seen as low down as the brains of the monotremes. The Sylvian fissure, on the other hand, belongs to the pallium. It is not seen in the smooth-brained *Ornithorhynchus*, or in the lissencephalous rodents, insectivores, or bats. In *Echidna*, again, the small fissure, marked *s* in fig. 9, may perhaps represent a Sylvian fissure. In *Macropus major* I think it is possible that the middle vertical transverse fissure is a Sylvian fissure. The radiating character ot these fissures in the brains of *Macropus* and *Halmaturus*, in which it must be remembered the corpus callosum is rudimentary, is of interest in connection with the radiated arrangement of the transitory fissures on the cranial surface of the human brain at an early stage of development.[1] In *Hyrax* the more anterior vertical transverse fissure is also perhaps to be regarded as representing a Sylvian fissure, though it does not reach the rhinal fissure. It would appear, therefore, that in the evolution of the brain in the mammalian series the Sylvian fissure may be present in the brains of such low mammals as *Echidna* and *Macropus*, which are also convoluted, whilst it is absent in the smooth-brained rodents, bats, and insectivores—mammals that in other respects are more highly organised than the monotremes and marsupials. Further, in these lissencephala there is a tendency for a sagittal fissure and a marginal convolution to differentiate on the cranial surface before there is any evidence of a Sylvian fissure being present.

But the mesial surface of the pallium is also of interest in connection with the appearance in it of fissures and convolutions.

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[1] See an interesting discussion on these "complete" fissures in the human brain by Professor D. J. Cunningham in *Journal of Anatomy and Physiology*, April 1890.

The fundamental character of the fissura hippocampi and gyrus dentatus has already been pointed out, and in the brains of *Ornithorhynchus* and the *Insectivora* they are apparently the only parts which are morphologically differentiated. In some rodents, however, traces appear of a longitudinal fissure situated in the grey cortex above the corpus callosum, which is more accentuated in the bats *Cynonycteris* and *Pteropus*. It is named sometimes the splenial, at others the limbic, fissure (*sp*). This fissure is seen also in *Echidna*, in Marsupialia, in *Dasypus* and *Cholœpus*; and when it exists it differentiates a callosal from a marginal convolution. Moreover, when it is prolonged backwards and downwards to the tentorial surface of the pallium, it differentiates the posterior limit of a gyrus hippocampi. In the smooth-brained mammals, in which it is present, it is differentiated before a Sylvian fissure appears in them. In *Hyrax*, although the cranial surface is well convoluted, and a genual fissure is present in front of the corpus callosum, yet the splenial fissure, properly so called, is not differentiated. In these lower mammals, therefore, it would seem that the relative order in which the fissures make their appearance is not rigidly fixed, but that it varies in the different species.

From the description already given, it will have been seen that the fissures and convolutions are not uniform in their direction and arrangement, but that three leading groups, which may be described as sagittal or longitudinal, vertical transverse or coronal, and arcuate, may be recognised. The sagittal or longitudinal group lie parallel to the mesial longitudinal fissure; the vertical transverse lie on the surface of the pallium, and are directed from the mesial longitudinal fissure towards the rhinal fissure; and the arcuate group pursue a curved course from before backwards. All these groups assume more strongly marked characters in the more highly convoluted brains.

The orders in which the pallium assumes the most complex arrangement of convolutions are the Proboscidea,[1] Ungulata,

[1] Mayer (*Nova Acta*, vol. xxxii.) has given a figure of the brain of the Indian Elephant; Leuret also has figured the convolutions. Krueg has figured that of the African Elephant (*Zeitsch. f. wiss. Zool.*, vol. 33, pl. xxxviii.). In the Museum of the Royal College of Surgeons, England, is a beautiful specimen, which has not, I believe, been described.

Cetacea, Carnivora, Pinnipedia, and Primates with Homo.[1] But even in some of these orders there are a few species in which the pallium is either smooth or only feebly convoluted. This is especially the case in the smaller species of these orders, where the weight of the body is small, but where the brain is relatively larger to the body than is the case in the larger species of the same order. A central sensori-motor apparatus of sufficient magnitude for the requirements of the animal can thus be accommodated in a cortex possessing a plane surface, and the need for a convoluted folding of that surface does not arise. The most striking examples of smooth-brained mammals, in an order otherwise gyrencephalous,[2] is seen in the little Marmoset Monkey (fig. 36),[3] a genus of Primates.

To describe in detail the arrangement of the convolutions in gyrencephalous mammals would occupy much more time than is at my disposal, so that I shall limit myself to directing attention to the more striking general features in the plan of construction.

Convolutions and fissures extending in a direction which may be termed antero-posterior, sagittal, or longitudinal are to be seen. Invariably, I think I may say, the margin of the mesial longitudinal fissure, for either the whole or a considerable part of its length, is bounded by such a convolution, which is partly situated on the cranial and partly on the mesial surface of the pallium, and which is appropriately called marginal (*m*). In Man and the more highly convoluted Apes tiers of antero-posterior convolutions, with their intermediate fissures, make up a large portion of the frontal lobe.

[1] Comparatively little is known of the brain in the Sirenia. Dr Murie, in his well-known Memoir on the Manatee, figures the cerebrum as possessing both a rhinencephalon and a pallium. The pallium has a deep Sylvian fissure, and the cortex is marked by shallow fissures indicative of convolutions. The specimen was not in good order (*Trans. Zool. Soc.*, vol. viii.). Mr A. H. Garrod examined the brain of a Manatee twenty-four hours after death. He describes a Sylvian fissure, a hippocampal fissure, and a calloso-marginal (splenial) sulcus with indications of a superior frontal sulcus. He states that the brain does not present convolutions properly so called (*Trans. Zool. Soc.*, vol. x.).

[2] This term, as well as the term lissencephala in other parts of the text, is used only in its descriptive sense, and not as a taxonomic expression.

[3] Owen says that the weight of the midas Marmoset is to its body as 1 to 20; that of the Gorilla as 1 to 200.

The Sylvian fissure, common to all the gyrencephala, may, I think, be regarded as fundamentally vertical transverse in direction, though in some brains, especially in Man and the higher Apes, it is directed very obliquely backwards. Its length varies materially from a few mm., as in the smaller Carnivora and Ungulata, to several centimetres, as in Homo. Its depth also is variable, and in such brains as the Cetacea, Apes, and Man, where its depth is considerable, it more or less perfectly conceals a set of convolutions which constitute the insula or island of Reil.

In the Carnivora, Pinnipedia, Cetacea, and Ungulata certain convolutions and fissures are arranged in successive tiers in front of, above, and behind the Sylvian fissure, so as to assume a decidedly arcuate character. In the Carnivora they have been carefully studied in a large number of genera by many anatomists.[1] The most simple arrangement is to be seen in the smallest Carnivora, as the Ferret (*Mustela furo*) (fig. 17) and the domestic Cat (fig. 18), in which three simple convolutions arch above the Sylvian fissure, which may be named *Sylvian, supra-sylvian,* and *marginal,* whilst the intermediate arcuate fissures are *supra-sylvian* and *lateral.* The marginal convolution has more of an antero-posterior direction, and forms the longitudinal marginal convolution of the mesial longitudinal fissure. In the larger Carnivora, like the Tiger and Polar Bear (fig. 19), similar tiers are also to be seen; the convolutions also are not so simple, but more winding and more frequently subdivided by secondary fissures. In the Canidæ (fig. 20), four tiers of convolutions are met with, which

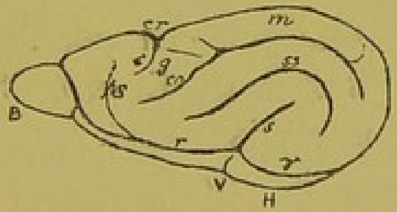

FIG. 17.—Cranial surface of hemisphere of *Mustela furo.*

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[1] I may especially refer to the writings of Owen, Leuret, Flower, Benedikt, Pansch, and Krueg; also to my chapter on the Convolutions of the Brain in *Challenger Reports,* "Zoology," part lxviii., reprinted in *Journal of Anatomy and Physiology,* vol. xxii., 1888.

may be termed Sylvian, supra-sylvian, lateral, and sagittal or marginal, whilst the additional fissure may be named *medio-lateral.* In the Pinnipedia four tiers of convolutions are also present, and their tortuosity is more marked than in the proper Carnivora (fig. 21). Both in the Elephant Seal and Walrus, the Sylvian convolution is partially sunk into the Sylvian fissure, and I have seen a similar arrangement in the brains of the Otter (*Lutra vulgaris*) and the Badger (*Meles taxus*).

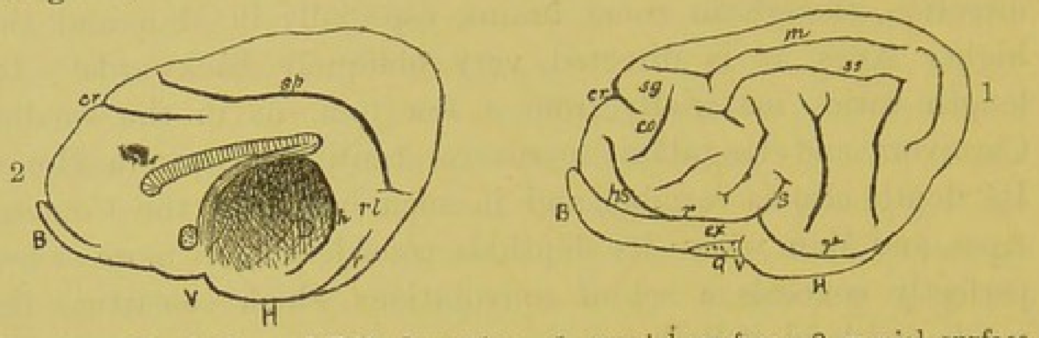

Fig. 18.—Hemisphere of *Felis domestica.* 1, cranial surface; 2, mesial surface.

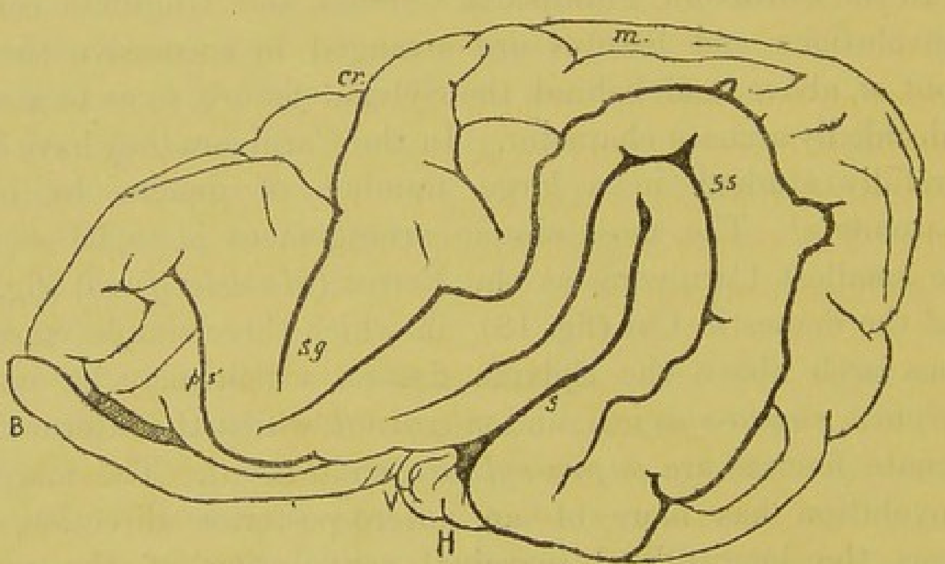

Fig. 19.—Cranial surface of the hemisphere of *Ursus maritimus.*

In the Carnivora and Pinnipedia special names are applied to certain of the fissures on the cranial surface. A fissure, which springs from the neighbourhood of the Sylvian fossa or the rhinal fissure in front of that fossa, and which runs forwards and upwards on the cranial surface of the more anterior part of the pallium, is called the *præ-sylvian fissure* (*p.s.*). Owen gave the name *coronal fissure* (*co.*) to a fissure which passes more or less in the coronal direction down the cranial surface of the anterior part of the pallium. The coronal fissure may, as in the Dog, or it may not, as in the Cat, be continuous with the lateral fissure, *i.e.*, the most superior of the arcuate fissures of the pallium. The name of *coronal convolution* is sometimes given to the more anterior part of the second external convolution which bounds the coronal fissure posteriorly. The part of the supra-sylvian fissure which lies behind the Sylvian convolution is sometimes named *fissura supra-sylvia posterior* (*ssp*). In the carnivorous brain another vertical transverse fissure, the *crucial fissure* (*cr*) of Leuret,

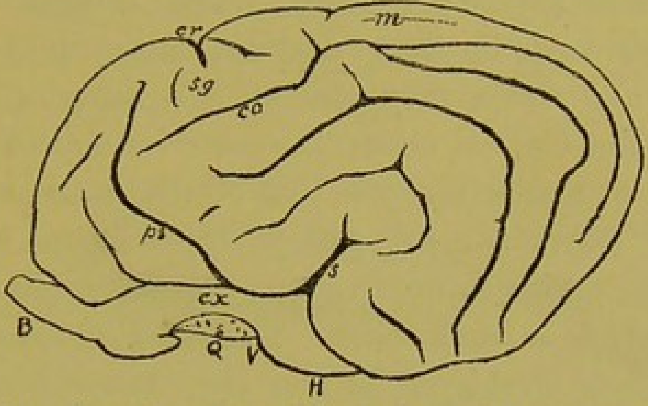

FIG. 20.—Cranial surface of hemisphere of *Canis familiaris*.

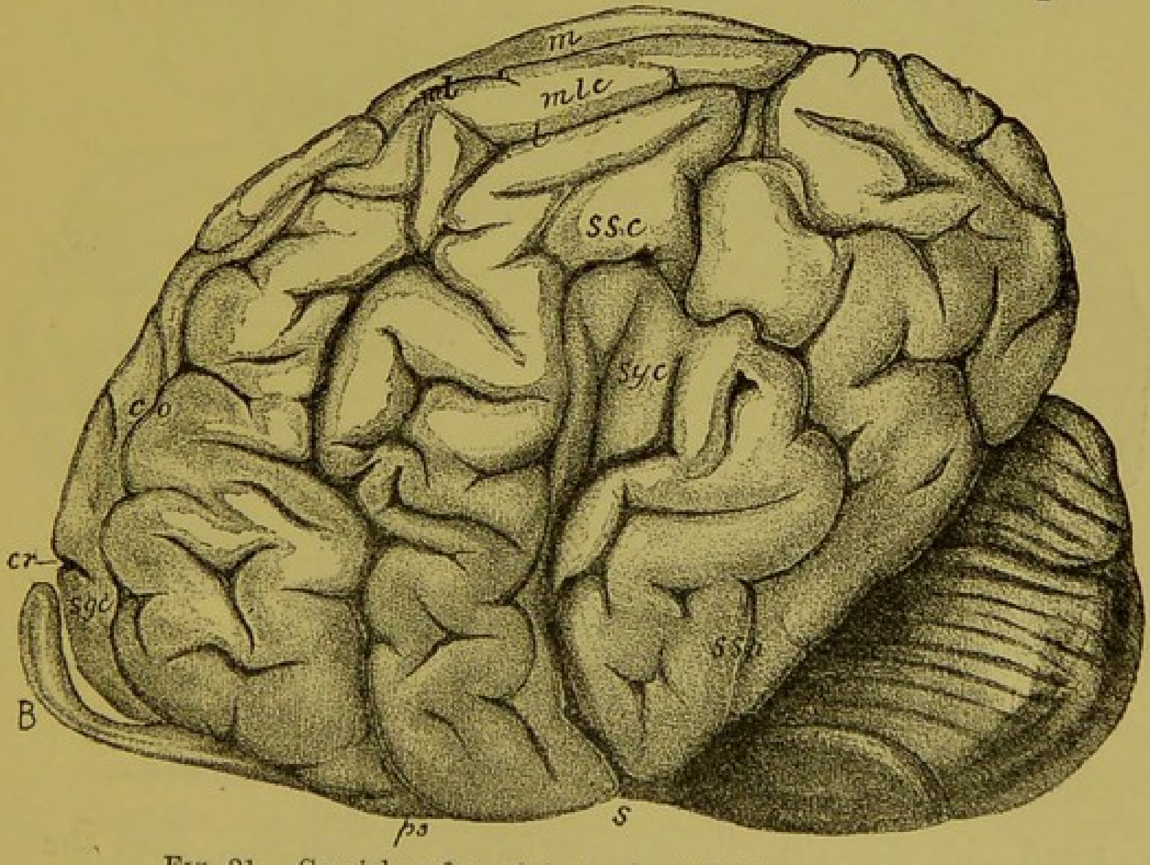

FIG. 21.—Cranial surface of the brain of *Trichechus rosmarus*.

is very characteristic. It extends from the mesial longitudinal fissure almost transversely outwards and is bounded by the *sigmoid gyrus* (*sg*) of Flower. The crucial fissure and sigmoid gyrus vary in their position antero-posteriorly. In the Walrus and Seals they are at the anterior end of the pallium; in the Cat in about the anterior fourth, in the Dog and Mustela at nearly the junction of the anterior and middle third, in the Bears at nearly the junction of the anterior and posterior half. The sigmoid gyrus separates the crucial and coronal fissures from each other. The most anterior end of the pallium, in such Carnivora as the Dog, has a beak-like form, and has been named the *prorean convolution;* whilst the fissure which forms its posterior boundary, situated in front of and almost parallel to the præ-sylvian fissure, is the *prorean fissure* of Krueg.

The mesial surface of the carnivorous cerebrum has a distinct *splenial fissure,* which has a longitudinal and arcuate arrangement (figs. 18, 19). It differentiates the marginal from the callosal convolution, and as the callosal is continued behind into the hippocampal convolution, these two form the great arcuate gyrus fornicatus. A fissure bent downwards in front of the

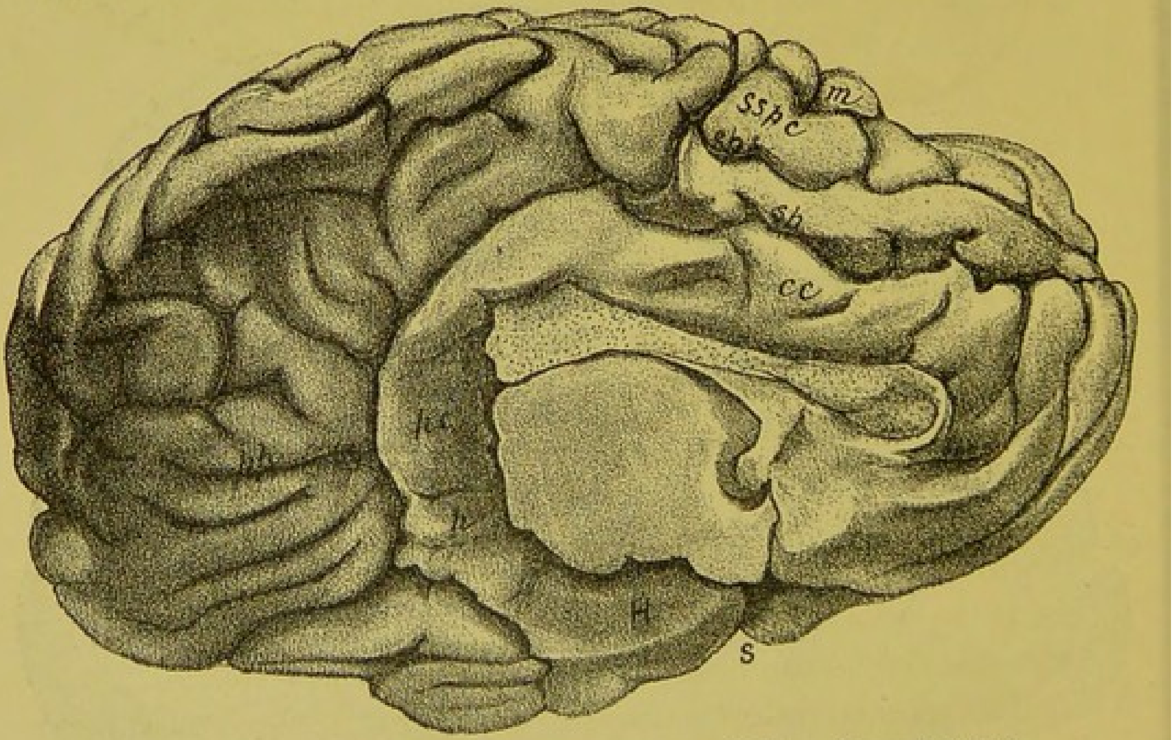

FIG. 22.—Mesial surface of left hemisphere of *Macrorhinus leoninus.*

genu of the corpus callosum is sometimes continued back into the splenial fissure, but at other times is independent of it, in the latter case it is named the *genual fissure* (*g*). In the Elephant Seal (*Macrorhinus*) the pallium above the splenial fissure is divided by a *supra-splenial fissure* into two tiers

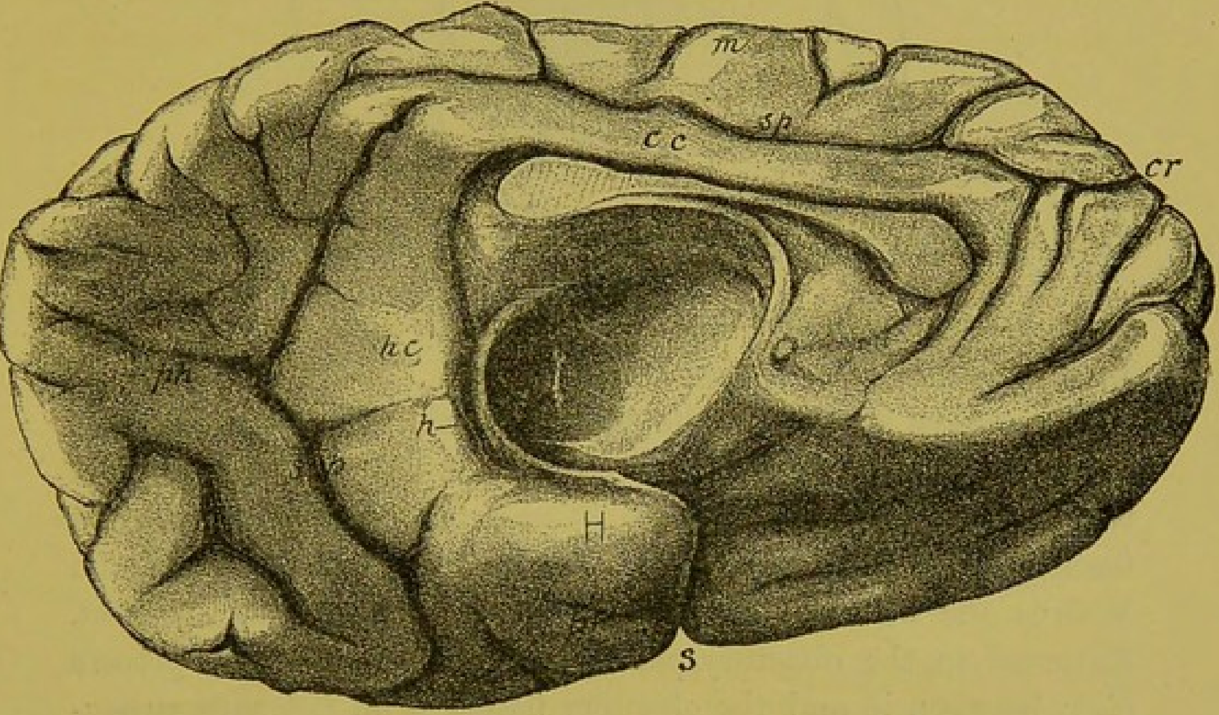

FIG. 23.—Mesial surface of left hemisphere of *Trichechus rosmarus*.

(fig. 22) named the *marginal* and *supra-splenial convolutions*. In the hemisphere of the Walrus, represented in fig. 23, this division has not taken place, but in another specimen both the supra-splenial fissure and convolution are present. Both in the Walrus and Elephant Seal a *postero-horizontal fissure* (*ph*) extends backwards from the splenial fissure. Below the postero-horizontal fissure a distinct *post-splenial fissure* (*psp*) (Krueg) is to be seen, and between it and the postero-inferior part of the splenial fissure is a *splenial convolution* (*spc*).

The splenial fissure varies in its relation to the crucial fissure in the carnivorous brain. In the Elephant Seal, Walrus, various Canidæ, Badger, Ratel, Mustela, I have observed them to be continuous with each other; whilst in Phoca, Ursus, Coati, and some Felidæ, I have seen them to be separated by an intermediate convolution.

In the brain of the Dog the splenial fissure is not unfrequently prolonged into the most posterior part of the rhinal fissure (fig. 24). In the Carnivora generally these fissures are most usually separated from each other by a convolution which Broca has named *retrolimbic* (fig. 18, *rl.*)

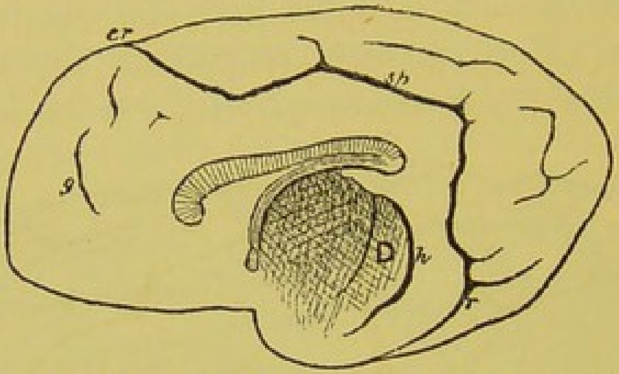

Fig. 24.—Mesial surface of right hemisphere of *Canis familiaris.*

The orbital surface of the pallium in the Carnivora possesses a distinct *olfactory fissure,* which is concealed by the bulb of the rhinencephalon; between it and the mesial longitudinal fissure is a *gyrus rectus.* In the Elephant Seal (fig. 2) and Walrus the olfactory fissure and gyrus rectus are also present. External to the olfactory peduncle is an *intra-orbital fissure* (*io*); between it and the olfactory fissure is an *internal supra-orbital gyrus* (*isc*), and between it and the præ-sylvian fissure is an *external supra-orbital gyrus* (*esc*).

In the brains of the Ungulata the cranial surface of the pallium shows a Sylvian fissure surmounted by tiers of arcuate fissures and convolutions. The laborious researches of Krueg,[1]

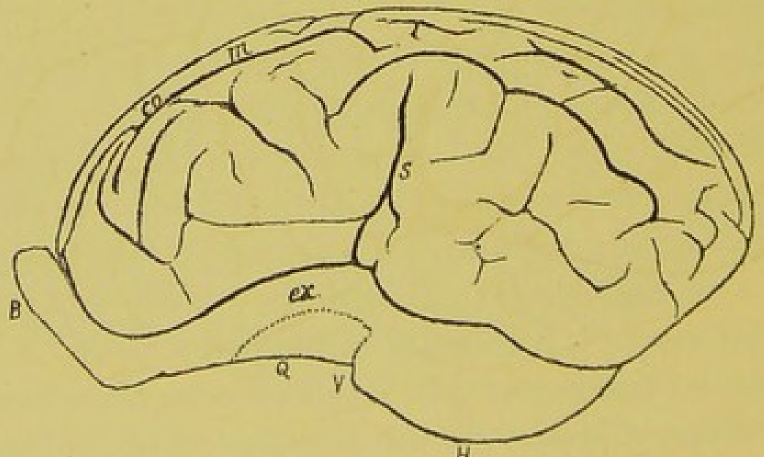

Fig. 25.—Cranial surface of hemisphere of *Ovis aries* (Sheep).

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[1] *Zeitsch. f. wissen. Zoologie,* vol. xxxi. 1878.

have demonstrated the presence of at least three tiers of convolutions in a large number of species. The highest tier forms the marginal convolution of the mesial longitudinal fissure. This arrangement is seen in the Sheep (*Ovis aries*) (fig. 25). In some species, as the Ox and Horse, four tiers of convolutions, with corresponding fissures, are present, which may be named in terms similar to those employed in the nomenclature of the Dog's brain. Both coronal and præ-sylvian fissures exist in the ungulate brain. Some anatomists hold that a crucial fissure may

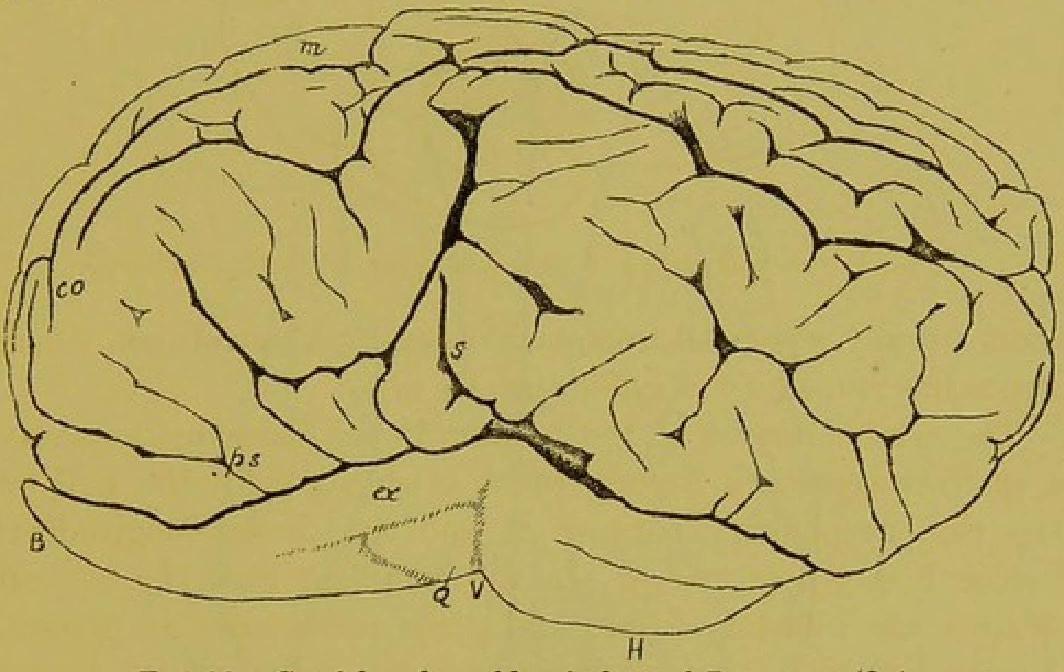

FIG. 26.—Cranial surface of hemisphere of *Bos taurus* (Ox).

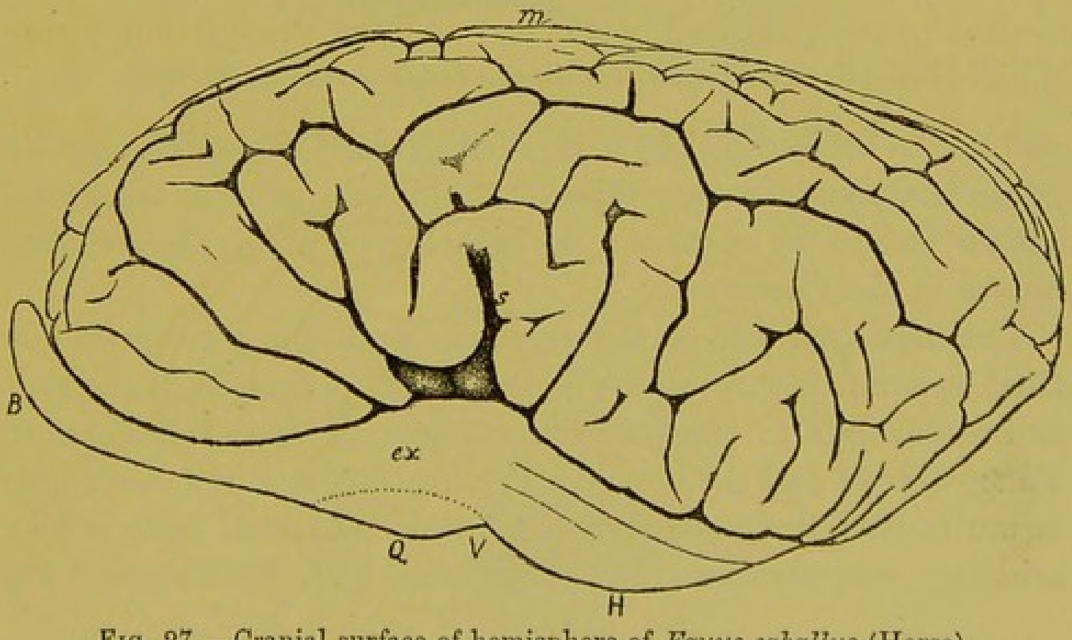

FIG. 27.—Cranial surface of hemisphere of *Equus caballus* (Horse).

also be recognised. In the Suidæ, more especially in *Dicotyles*, a fissure runs transversely outwards from the mesial longitudinal fissure; at first sight it might be taken for a crucial fissure, but on closer observation it will be seen to join the coronal fissure, and not to be bounded by a sigmoid gyrus. When the sigmoid gyrus is absent, I do not think that this or any other transverse fissure should be regarded as homologous with the cruciate fissure in the Carnivora.

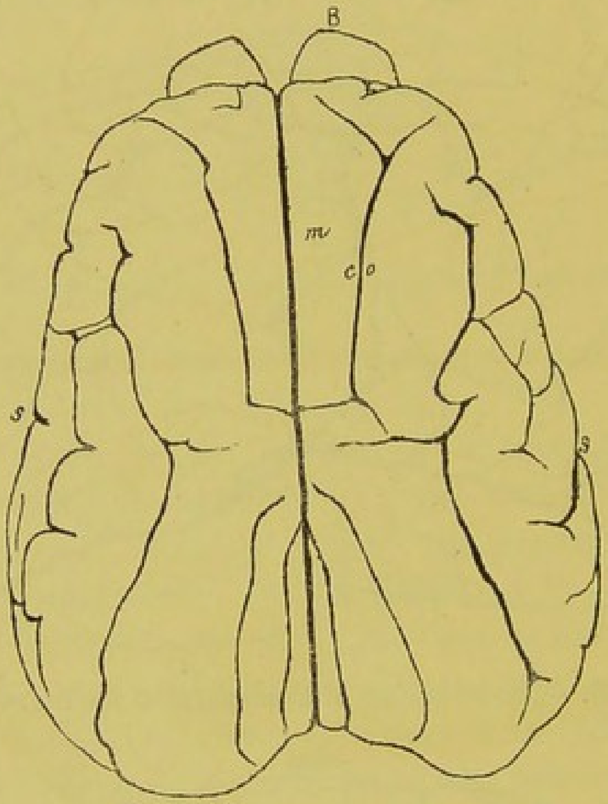

FIG. 28.—Vertex view of brain of *Dicotyles torquatus* (Peccari).

The mesial surface of the ungulate cerebrum possesses a distinct splenial fissure, which is frequently prolonged backwards and downwards to the tentorial surface; in many species, as in *Phacochœrus* and the common Pig (fig. 30), it is not continued forwards into the genual fissure, but is separated from it by a bridging convolution. In the Horse and Rhinoceros,[1] the

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[1] Owen described and figured the brain of the Indian Rhinoceros (*R. unicornis*) in *Trans. Zool. Soc.*, 1850, and Garrod figured the brain of the Sumatran Rhinoceros in *Trans. Zool. Soc.*, vol. x. pl. lxx., and in Collected Scientific Papers. The brain of the Hippopotamus has been described by Peters (*Monats. d. Berliner Akad.*, 1854); Gratiolet, Paris, 1867; Macalister, *Proc. Roy. Irish Acad.*, vol. i., 1873-74; Garrod, *Trans. Zool. Soc.*, vol. xi., and in Collected Scientific Papers.

callosal convolution is partially divided into two tiers by a longitudinal fissure. The splenial fissure not unfrequently turns upwards to the margin of the pallium (fig. 30) to become continuous on the cranial surface with either the coronal or the

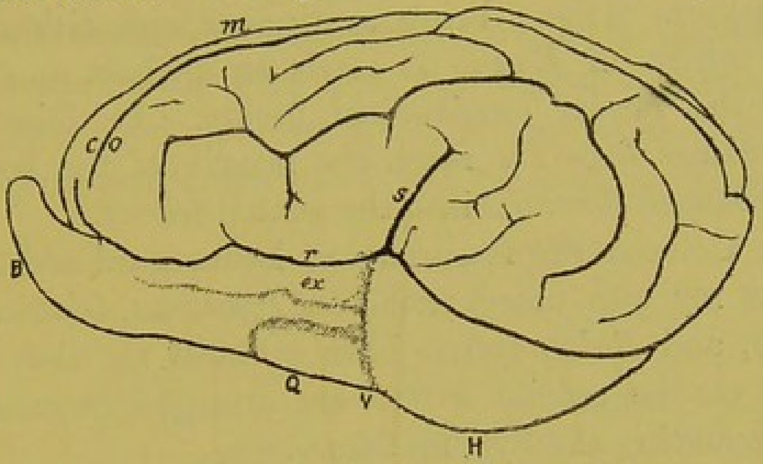

Fig. 29.—Cranial surface of hemisphere of *Sus scrofa* (Pig).

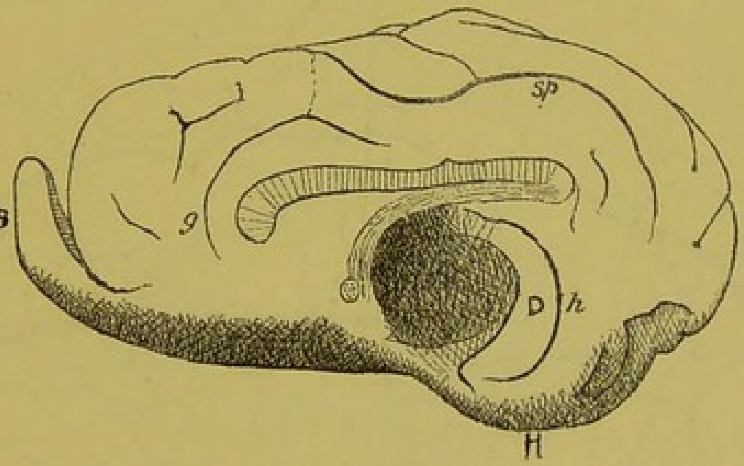

Fig. 30.—Mesial surface of hemisphere of *Sus scrofa*.

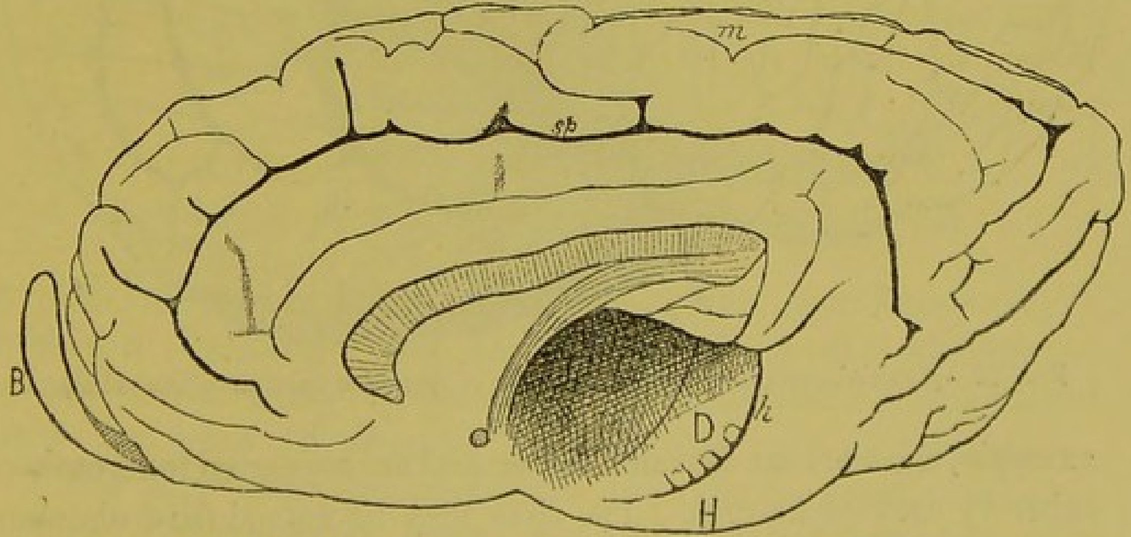

Fig. 31.—Mesial surface of hemisphere of *Equus caballus*.

lateral fissure, as in the Pig and Gazelle. I have seen in the brains of *Ovis* and *Bos* the splenial fissure reach the margin of the pallium without being continuous with either of these fissures; whilst in *Equus* it sends an offshoot as far as the edge of the mesial longitudinal fissure. In *Dicotyles* the splenial fissure does not reach the margin of the hemisphere, but is prolonged forwards into the genual fissure.

In the Cetacea the researches of Beauregard and Guldberg, as well as my own observations on *Phocœna, Globiocephalus, Monodon,* and *Balœnoptera* have satisfied me that the convolutions on the cranial surface are arranged in great arcuate tiers surmounting the Sylvian fissure.

In the Narwhal (*Monodon*), and in *Balœnoptera rostrata,* for example, the tiers are four in number, and are separated from each other by arcuate fissures. The tiers may be named from above downwards, marginal, medio-lateral, supra-sylvian, and Sylvian. Each of these tiers is in its turn broken up into secondary convolutions, so that the whole cranial surface of the pallium is

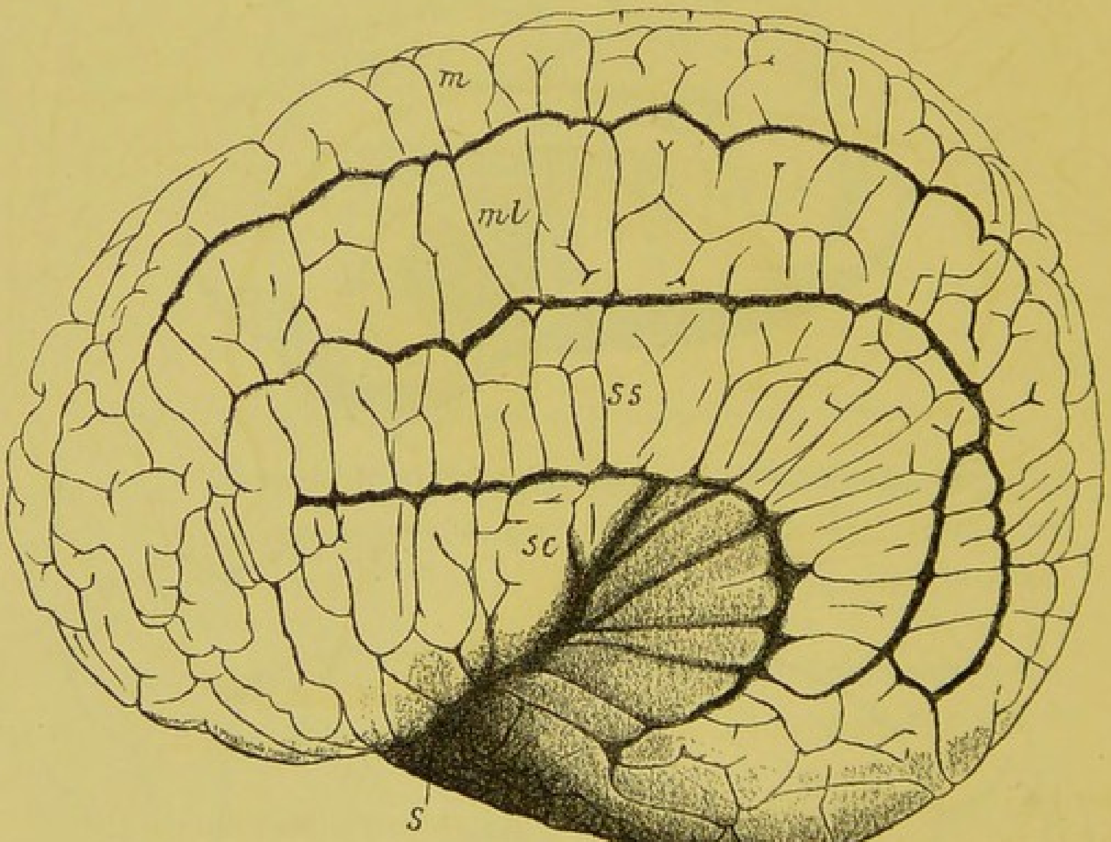

Fig. 32.—Cranial surface of the hemisphere of *Monodon monoceros* (Narwhal).

highly convoluted. Fissures which may be termed præ-sylvian and coronal may also be recognised.

The mesial surface of the hemisphere may be described from *Balænoptera rostrata* (fig. 33). The corpus callosum is surmounted by a gyrus fornicatus, which may be traced from the perforated or quadrilateral space as a great arcuate convolution, at first upwards and forwards as the callosal convolution (*cc*), and then backwards and downwards behind the splenium, where, as the gyrus hippocampi (*hc*), it becomes continuous with the lobus hippocampi. The callosal part of this convolution is partially subdivided into two tiers by a longitudinal fissure. The splenial fissure forms the upper boundary of the gyrus fornicatus in its whole length, and consists of the genual and splenial fissures continued into each other. It is crossed near the lobus hippocampi by two retro-limbic gyri.

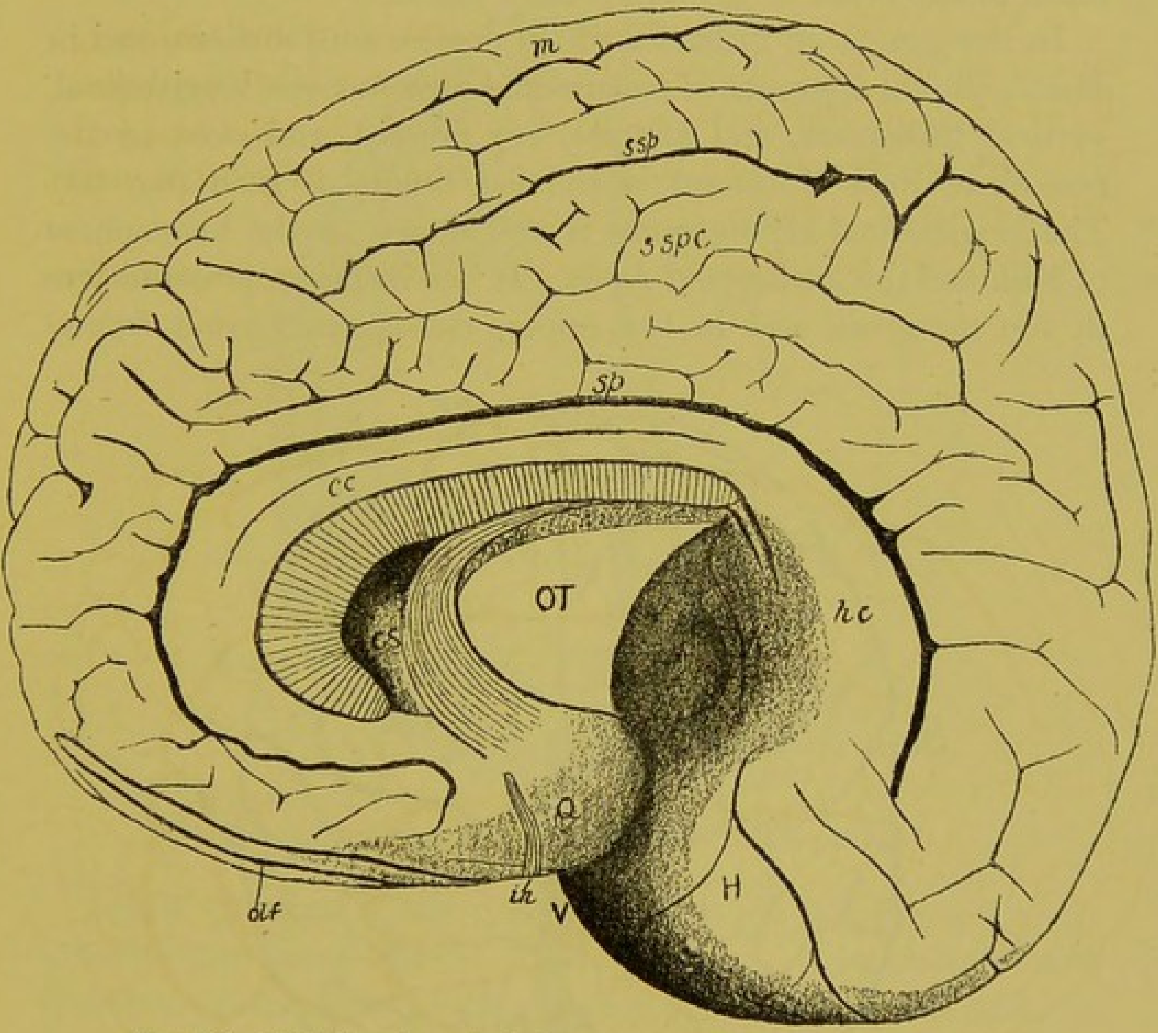

Fig. 33.—Mesial surface of the hemisphere of *Balænoptera rostrata.*

The inner face of the hemisphere above the splenial fissure has a high vertical diameter, is greatly sub-convoluted, and is divided by a supra-splenial fissure (*ssp*) into a supra-splenial and a marginal convolution. The tendency to the formation of secondary or tertiary convolutions is more marked in the cetacean than in any other brain, and it probably reaches its maximum in the brain of *Globiocephalus melas*.

In the genera of Primates which possess convolutions, and in Homo, the three groups of fissures and convolutions, longitudinal, vertical transverse, and arcuate, are present, and even in the smooth-brained Marmoset, a Sylvian fissure is seen (fig. 36). The longitudinal arrangement is well shown in the hemisphere of Man and the anthropoid Apes. It has its best representatives in the marginal, and in the upper, middle, and lower frontal convolutions. The arcuate arrangement is seen in the more posterior convolutions of the parietal lobe, which are continuous through the bridging convolutions with the convolutions of the occipital and the temporo-sphenoidal lobes. The Sylvian fissure is surmounted by these convolutions. The

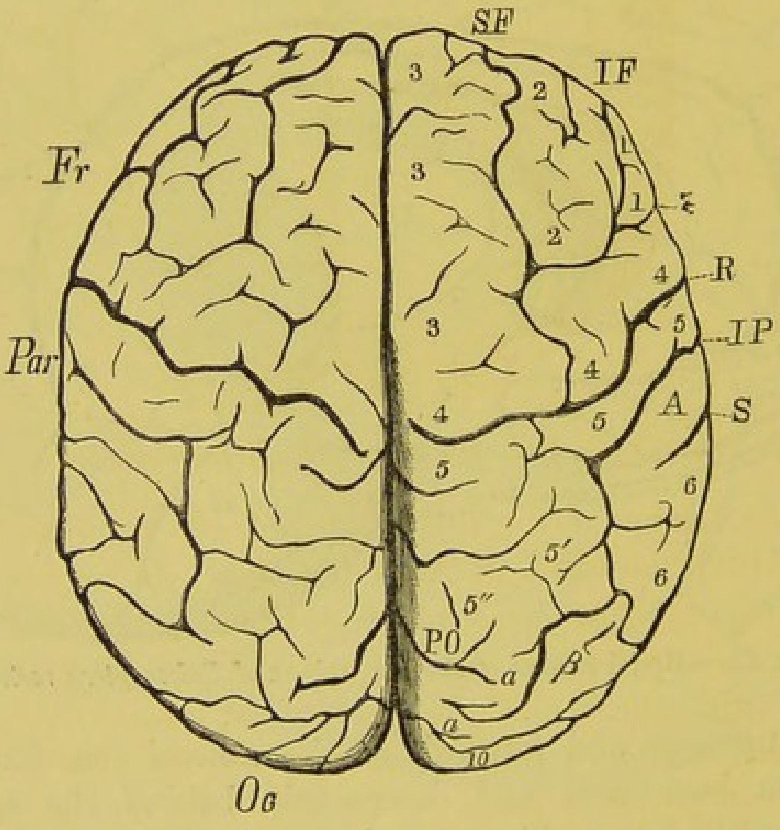

FIG. 34.—Vertex view of the human brain.

continuity of this arcuate arrangement with the convolutions of the frontal lobe is, however, disturbed by the magnitude and importance of the two great vertical transverse or central convolutions, named *ascending frontal* and *ascending parietal*, and of the *central fissure*, or *fissure of Rolando*, which lies between them (figs. 34, 35).

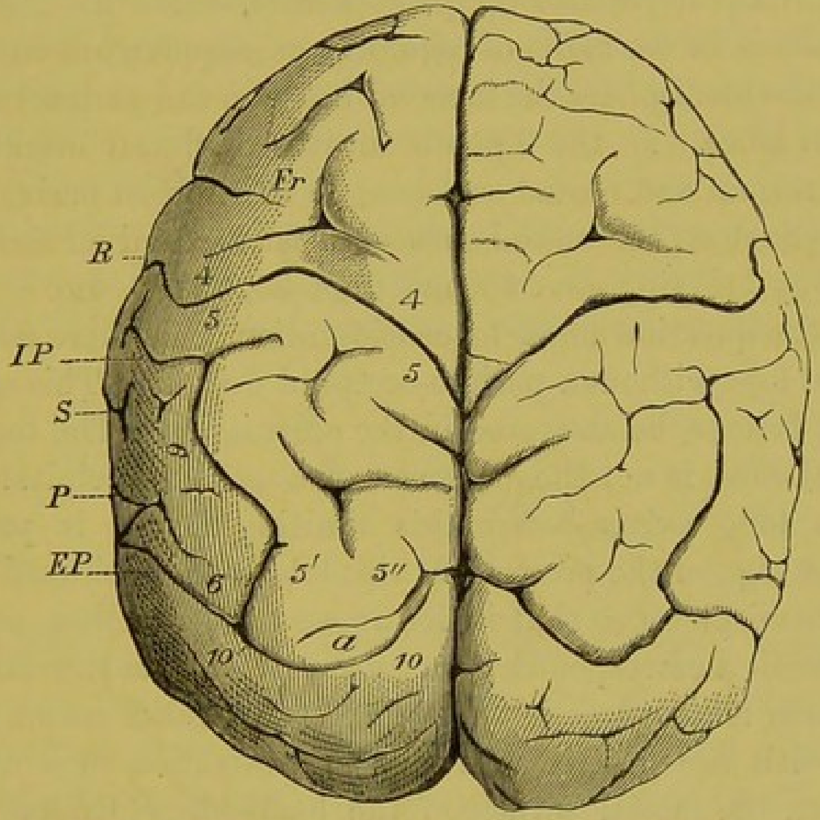

Fig. 35.—Vertex view of the brain of a Chimpanzee.[1]

It is a question if the fissure of Rolando is present in any other brains than those of Apes and Man. It has been looked for more especially in the carnivorous brain, and several opinions have been expressed on the subject. A certain similarity in direction with the crucial fissure has led several authorities to regard the fissure of Rolando as homologous with it, and the anterior and posterior limbs of the sigmoid gyrus as the homologues of the ascending frontal and parietal convolutions. Broca and other French anatomists again look upon the præ-sylvian fissure as representing the fissure of Rolando. Owen, Pansch, and Meynert have regarded the coronal fissure as the homologue

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[1] This figure and fig. 41 are reproduced from my memoir "On the Bridging Convolutions in the Brain of the Chimpanzee," *Proc. Roy. Soc. Edin.*, Feb. 19, 1866, p. 578.

of the fissure of Rolando, and several reasons, more especially of a physiological nature, may be urged in support of this position. I shall not, however, pursue the subject further on this occasion, as I have elsewhere discussed it at considerable length.[1]

But in the brains of the convoluted Apes and of Homo, another vertical transverse fissure of great importance has to be studied, viz., the *parieto-occipital fissure,* which the descriptive anatomist is in the habit of regarding as mapping out on the surface of the hemisphere the interval between the parietal and the occipital lobes. In the Ape's brain it is distinctly marked both on the cranial and mesial surfaces; in the human brain, though very distinct on the mesial surface, it is obscured on the cranial surface by bridging convolutions (figs. 34, 35, 40, 41).

But the question arises for consideration, Can there not be an occipital lobe without a parieto-occipital fissure? This question must, I believe, be answered in the affirmative. The test of an occipital lobe is not the presence of a parieto-occipital fissure, for the lobe exists before this limiting fissure is produced. The true sign of the presence of this lobe is the backward growth of the hemisphere, so that it lies above the cerebellum, and with this growth a corresponding extension of the ventricular cavity backwards takes place in the form of a posterior cornu. Associated with the posterior cornu is the formation of a calcarine fissure on the mesial surface of the hemisphere, through which is produced a calcarine elevation in that horn known as the hippocampus minor.

That this is the real explanation of the signification of the occipital lobe is proved by what is seen in the Marmoset Monkey (*Hapale jacchus*). In this animal the cerebrum is extended

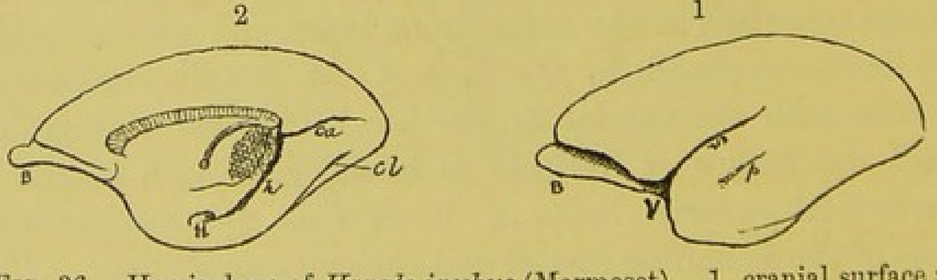

FIG. 36.—Hemisphere of *Hapale jacchus* (Marmoset). 1, cranial surface; 2, mesial surface.

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[1] See my "Memoir on the Seals" in the *Challenger Reports*, part lxviii., 1888, and in the *Journal of Anatomy and Physiology*, vol. xxxii. p. 554.

so far back as to cause the cerebellum to be below the hinder part of the cerebrum. On the cranial surface the Sylvian fissure is very distinct, and a shallow depression in the temporo-sphenoidal lobe marks the position of a rudimentary parallel fissure. Otherwise this surface is quite smooth. On the mesial surface there is no splenial fissure, but opposite the splenium a distinct calcarine fissure (fig. 36, *ca*) is continuous with the hippocampal fissure, and extends back almost as far as the tip of the posterior end of the cerebrum. Within the hemisphere a posterior cornu and calcar avis are present. There is no trace of a parieto-occipital fissure.

Confirmation of this view can be obtained from the brain of the Prosimian Javan loris (*Stenops*), in which a calcarine fissure on the mesial and tentorial surface proves the presence of both posterior cornu and calcar avis, *i.e.*, of an occipital lobe. In this animal there is no parieto-occipital fissure. Moreover, *Lemur nigrifrons* exhibits a similar arrangement (figs. 37, 38, *ca*).

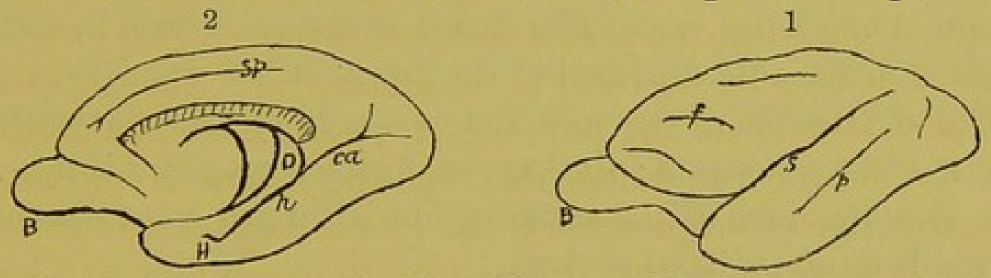

FIG. 37.—Brain of Stenops (after Flower).[1] 1, cranial surface; 2, mesial surface.

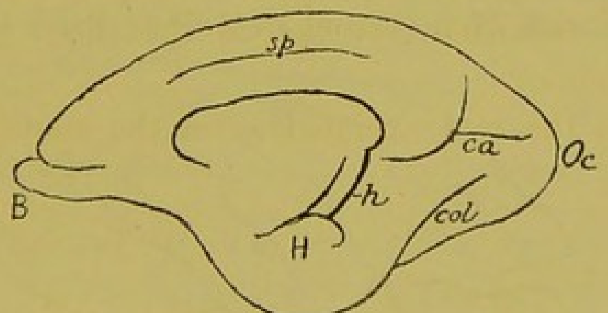

FIG. 38.—Hemisphere of *Lemur nigrifrons*, mesial surface (after Flower[1]).

Hence, if the surface of the hemisphere be examined with the view of determining the presence of an occipital lobe by the existence of a fissure, the calcarine fissure is that which is to be regarded as of primary importance, and the parieto-occipital fissure appears at a later period in the evolution of the mammalian brain. What then is the signification of the parieto-

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[1] *Trans. Zool. Soc. Lond.*, vol. v. 1862.

occipital fissure? It is, I believe, nothing more than a folding on the cranial and mesial surfaces of the hemisphere, expressive of and due to the great development of the grey matter of the cortex and its associated white matter in the region where the posterior cornu branches backwards from the body of the ventricle. This fissure is absent in the Prosimii and in the Platyrrhine Marmoset, but it is present in Man, the Apes of the Old World, and in the larger American Monkeys as *Pithecia Ateles*, and *Cebus*.

From this view of the case I cannot, as is done by some anatomists, regard the occipital lobe as a bud, more or less independent, springing out of the hinder part of a parietal lobe and separated from it by a constricting fissure. In my judgment the occipital lobe is due to a continuous growth of the hemisphere and of the ventricular space contained within it, correlated with an antero-posterior elongation of the cranial cavity, and a depression downwards and forwards of the cerebellum and medulla oblongata; so that the foramen magnum is not at the posterior end of the cranium, but is thrown some distance forwards on to its basal surface.

The period of appearance, in the course of the evolution of the mammalian brain, of a fissure of Rolando, having a position and direction such as we are familiar with in the brains of Primates, may also engage our attention for a few moments.

In the Prosimian *Stenops* and *Lemur nigrifrons* it is absent.

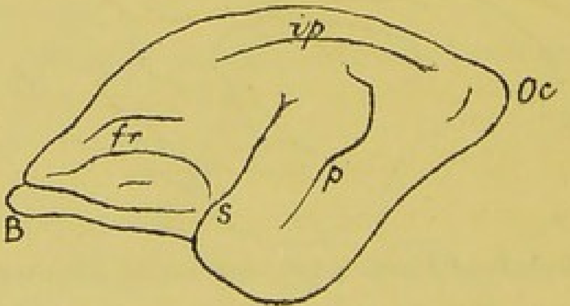

FIG. 39.—Hemisphere of *Lemur nigrifrons*, cranial surface (after Flower).

No vestige of it can be seen in the Platyrrhine Marmoset; but it is distinct in the Platyrrhine genera, *Pithecia*, *Ateles*, *Cebus*, &c. But, notwithstanding its absence in the *Lemuridæ* and the smaller Apes of the New World, there can be no question, from the general conformation of the hemispheres in these animals, that they contain potentially both frontal and parietal lobes. It is true that the Marmoset has a perfectly smooth hemisphere in front of and above the Sylvian fissure; but the hemisphere in *Stenops* possesses in its more anterior part rudimentary fissures extending antero-posteriorly, which mark the commencement of a differentiation into tiers of convolutions extending in a sagittal direction, such as one is familiar with in the frontal lobe of the higher Apes. Corresponding antero-posterior fissures exist also in *Lemur nigrifrons* (fig. 39, *fr*), and another fissure is placed further backwards (*ip*), which is probably the homologue of the intraparietal fissure in the higher brains. Hence we cannot but conclude that a cerebral hemisphere may possess both a frontal and a parietal lobe, even when no trace of a fissure of Rolando exists, just as it may have an occipital lobe without a parieto-occipital fissure.

A distinct temporal lobe also exists in the Prosimian brain, and both in *Lemur nigrifrons* and *Stenops* a fissure parallel to and behind the Sylvian fissure may be seen in this lobe. Even in the smooth-brained Marmoset a temporal lobe elongated downwards and forwards is present, and a rudimentary parallel fissure can be recognised; whilst in the larger American Monkeys, like *Cebus* and *Ateles*, and still more in the Old World Apes and in Man, the general characters of this lobe are known to all anatomists.

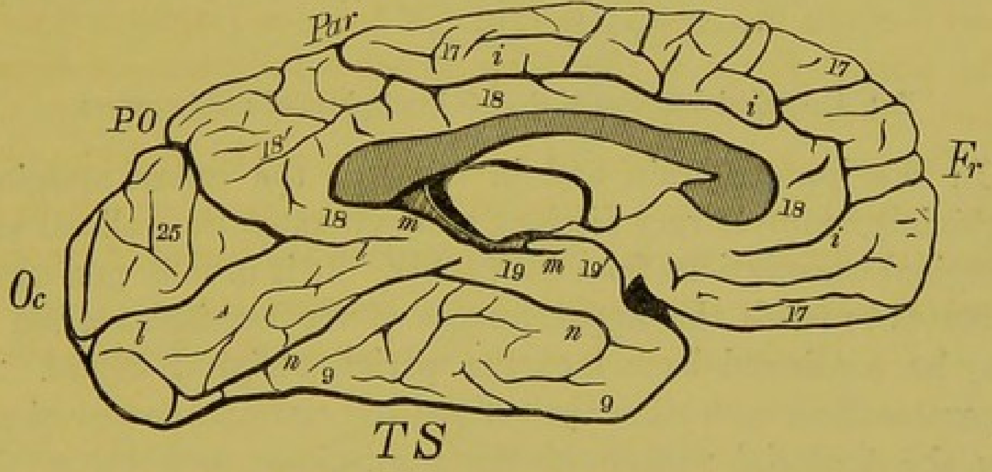

FIG. 40.—Mesial surface of the left hemisphere of Man.

Both *Lemur nigrifrons* and *Stenops* possess a calloso-marginal or splenial fissure, so that the marginal convolution is differentiated from the callosal (figs. 37, 38), whilst in the

Platyrrhine Marmoset this fissure is absent, and the callosal and marginal areas of the mesial aspect of the hemisphere present a continuous plane surface (fig. 36). In this respect, the *Lemuridæ* are in advance of the genus *Hapale* and more closely approximate to the arrangement found in the higher Apes and in Man.

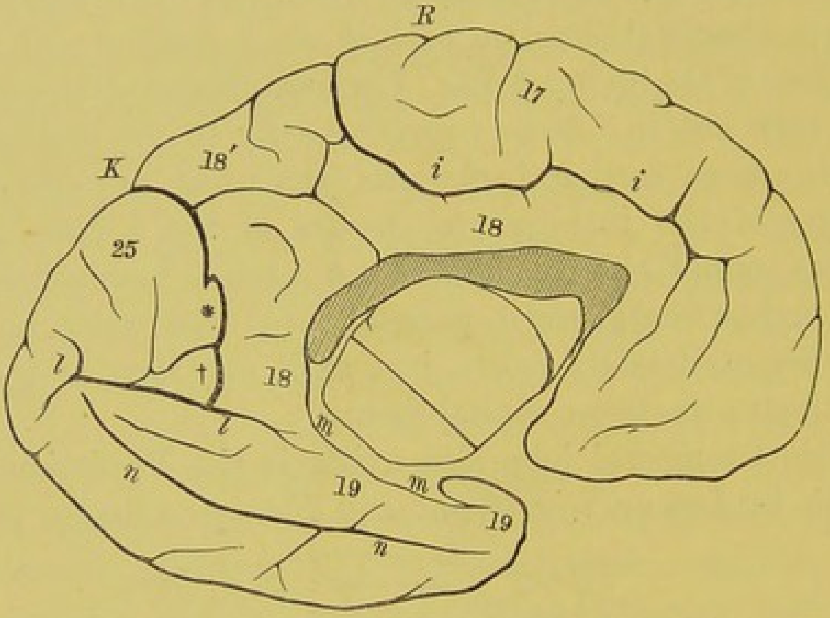

Fig. 41.—Mesial surface of the left hemisphere of a Chimpanzee.

In the human brain and in the Ape the calloso-marginal (splenial) fissure is very distinct, and separates the callosal and marginal convolutions from each other. It is usually prolonged upwards to reach the upper margin of the hemisphere, and it may be continued back into the parieto-occipital fissure. It separates from each other the callosal and marginal convolutions. On the tentorial surface of the hemisphere, and below the calcarine fissure, is the *collateral fissure* (*n*), which forms the posterior boundary of the hippocampal convolution[1] (figs. 40, 41).

In the human brain and that of the Ape, more especially the anthropoids, the orbital surface of the frontal lobe is divided by fissures into convolutions. A distinct olfactory fissure which demarcates a gyrus rectus (fig. 42, 17) is present. External to

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[1] The calloso-marginal fissure in the human brain is apparently the conjoined genual and splenial fissures which in many lower mammals are not continuous with each other. When prolonged into the collateral fissure, as is frequently the case in Man and the higher Apes, it then forms a great arcuate fissure forming the upper boundary of the gyrus fornicatus, for which Waldeyer has suggested the name *sulcus fornicatus*.

the olfactory peduncle is a branching fissure which many years ago I named the *triradiate fissure.* The term intra-orbital fissure is, however, more appropriate, and the convolutions bounding it externally and internally, may be named, as in the Walrus and Seal, internal and external supra-orbital.

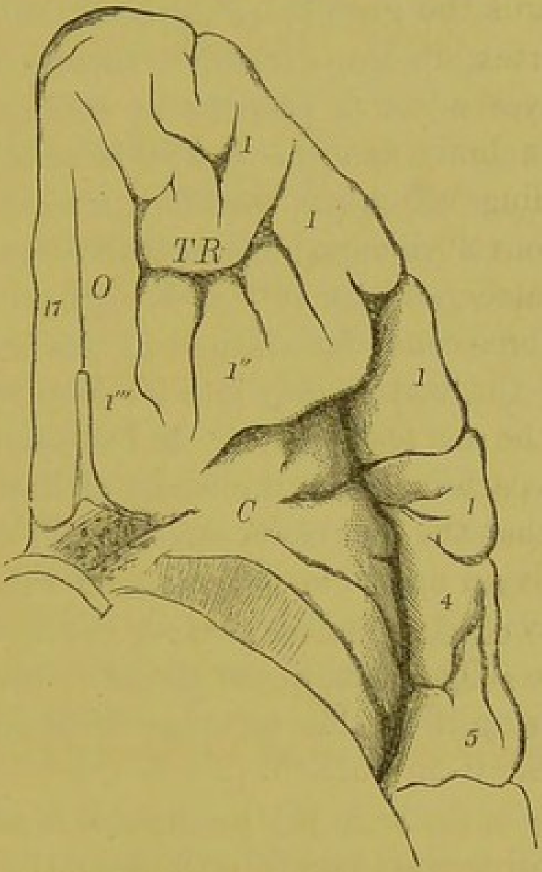

FIG. 42.—Orbital surface of the microsmatic brain of Man.

The consideration of the production of the fissures of the cerebral hemispheres, and the consequent conversion of a smooth brain into one with convolutions, is a matter of so much interest that I cannot conclude without making some reference to it. I believe that the mode of production of a convoluted surface is to be regarded as in the main a physical problem and to be studied from that point of view. Three great factors require to be taken into consideration in the discussion of this problem. *First,* the growth of the grey matter of the cortex and its associated white matter. *Second,* the growth of the great ganglia at the base of the hemisphere and the connections which these ganglia have through the intermediate strands of nerve-fibres with the cortical grey matter. *Third,* the pressure on the hemisphere due to the resistance offered by the parts which enclose it.

As regards the growth in superficial area of the grey matter of the cortex, it is universally recognised that a convoluted surface gives a much more extensive superficial area to the cortex of a brain than it is possible to obtain in a brain of a corresponding volume when the cortex is smooth. The presence of convolutions expresses, therefore, a more extended area of grey matter, and a corresponding modification in the strands of nerve-fibres connected with it.[1] It is very probable that this growth of the cortex may be affected by the tension exercised on it by the nerve-fibres passing into its deep surface from the subjacent parts of the encephalon. It has been suggested, for example, that the depression of the island of Reil at the bottom of the Sylvian fissure is due to its relation and connection with the subjacent corpus striatum checking its extension towards the surface. The cortical matter forming the lips of the Sylvian fissure, having no such check, would therefore project beyond it, and conceal it in such brains as those of Man, Apes, and the Cetacea.

But another chief factor in the production of the convolutions may be looked for in a resistance offered to the growth of the cortex along certain lines or planes. The parts which, from their situation, might be regarded as capable of offering such resistance are the blood-vessels of the pia mater; also the dura mater and the bones which form the walls of the brain cavity.

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[1] The influence which the convolutions have on the relation between the superficial area and the volume of the brain is expressed by M. Baillarger as follows:—"La différence entre le rapport des volumes et des surfaces est le résultat de cette loi mathématique; que les volumes des corps semblables sont entre eux comme les cubes de leurs diamètres, tandis que leurs surfaces sont entre elles comme le carré de ces diamètres, ce qui donne des proportions très différentes. Le cerveau subit cette loi à laquelle il est cependant soustrait en partie par l'existence des circonvolutions."—Quoted by M. Broca in his essay "Le Grand Lobe Limbique, &c.," *Revue d'Anthropologie*, 1878.

When this address was delivered in Berlin I had not seen the report in the *Brit. Med. Jour.* of Aug. 2, of the address delivered by Prof. Cunningham of Dublin at Birmingham in the previous week, in which the influences which produce the cerebral convolutions are discussed at considerable length, and the various theories which have been advanced are stated with force and lucidity.

As regards the possibility of pressure being effected by blood-vessels, the following reasons may be given:—

It is well known that, in several parts of the body, grooves may be produced by the pressure-pulsation of blood-vessels even on the bones themselves. Thus the arteria facialis can groove the inferior maxilla, and the arteria subclavia the 1st rib. Veins also may by pressure occasion grooves such as are produced by the lateral and superior longitudinal venous sinuses in the inner table of several of the cranial bones. Much more, therefore, is it possible to conceive that the pressure of the vessels of the pia mater may produce furrows on the surface of the soft cerebral cortex. There is indeed no difficulty in satisfying oneself that furrows can be produced by this agency. Any one who carefully strips off the pia mater from the cerebrum of a smooth-brained animal may see branching furrows on the cortex corresponding to the arterial distribution in the pia mater. In the developing brain, also, the pressure of the choroid plexuses on those parts of the wall of the hemisphere-vesicle which consist almost, if not quite exclusively, of epithelium, causes an involution of the thin wall of the hemisphere towards the ventricle, and a consequent furrow or fissure on the surface. Even in the convoluted brains one may, in certain localities, obtain evidence of furrowing of the surface of the cortex by arterial pressure.

But, notwithstanding all these examples, I do not attach much importance to the influence of arterial pressure as a factor in the formation of those fissures which I have been describing on the surface of the cerebral hemispheres. If they were of fundamental importance in this connection, then the pattern of the cerebral fissures and convolutions should precisely correspond with the distribution of the blood-vessels, which is by no means the case. Even when a blood-vessel follows the line of a fissure, the association between them is in all probability because the fissure offers a convenient and easy passage for the vessel, and not because the vessel by its pressure produces the fissure. As is well known, the middle cerebral artery is lodged in the Sylvian fossa and fissure, the depth of which is, without doubt, determined by other conditions than the pressure of this artery and its branches. From the examination of the injected brain of a *Marmoset*, I have seen a main artery occupying for some distance the Sylvian fissure, and then leave the fissure to pursue a course entirely independent of it. The relation between them is clearly, therefore, of secondary importance. Similarly the larger arteries of the cerebellum have not a definite relation to the numerous folia and fissures into which its surface is divided.

The resistance offered by the walls of the cranial cavity, comparatively unyielding as they undoubtedly are in the earlier stages of development, and still more unyielding as the ossification of the cranial bones advances, offers, I believe, another explanation of the production of a convoluted surface. The cranial cavity, when viewed in its relation to brain-growth, is not one chamber but three chambers. The single large cavity observed in the macerated skull is divided, when the dura mater is in position, into three chambers,—a pair of superior chambers separated from each other by the falx cerebri, in which the two cerebral hemispheres are lodged, and a single inferior chamber separated from the two superior by the tentorium cerebelli, and destined for the lodgment of the cerebellum. The resistance offered by the walls of the chambers in which the hemispheres are contained is due partly to the vaulted roof of the skull, partly to the tense and resisting falx cerebri, and partly to the equally tense tentorium cerebelli. The vaulted cranial roof has a continuous arched surface, but, where it is joined by the attachment of the falx and tentorium, a very definite angle is formed, so that the chamber for each hemisphere is, when seen in vertical transverse section, triangular in its shape. At each angle of this triangular chamber the soft and easily-moulded grey cortex is subject to pressure on two aspects, so that if the growth of the grey matter and hemispheres generally is at a greater rate than the growth of the chambers in which they are contained, their surfaces would become folded, and the direction of these foldings would have a relation to the lines or planes of resistance.

The primary fissure of the entire cerebrum is the mesial longitudinal fissure, the formation of which, at a very early period of development, separates the originally single hemisphere-vesicle into two hemispheres. The researches of Mihalkovics have shown that the production of this fissure is associated with the development of the falx cerebri, which, by its growth, pressure, and resistance, produces a depression in the mesial plane of the hemisphere vesicle, which, as it increases in depth, leads to the formation of the longitudinal mesial fissure.

We have here, therefore, distinct evidence that pressure and resistance on the vertex of the embryonic cerebrum have produced a fissure which, in this case, extends in the longitudinal or sagittal direction.

But the examination of the fissures and convolutions already made has taught us that in each hemisphere fissures and convolutions, extending in a sagittal direction, *i.e.*, parallel to the great longitudinal fissure, are a very usual arrangement, and their production is, I believe, in part due to the growth of the hemisphere chamber in vertical diameter not keeping pace with the growth in the vertical direction of the cerebral cortex; so that the cortex folds on itself in the longitudinal or sagittal direction, *i.e.*, at right angles to the direction of the pressure.

The production of vertical transverse fissures and of convolutions having a corresponding direction may, in like manner, be due to the resistance offered to the antero-posterior growth of the hemisphere, owing to the length of the cranial cavity not being proportioned to the growth of the hemisphere in the same direction. A striking illustration of this is furnished by the brain of the Cetacea. As is well known, the cranial cavity in these animals is antero-posteriorly compressed, so that the sagittal diameter of the brain is much less than the transverse. Now, if we examine the hemisphere of such a cetacean as the Narwhal (fig. 32), we see that, in addition to the arcuate fissures and convolutions referred to in the descriptive part of this address, the surface of the hemisphere is crowded with fissures and convolutions, the general direction of which is vertically transverse, *i.e.*, at right angles to the direction of the pressure.

As regards the arcuate fissures and convolutions, it is possible that they may be modifications of a system of fissures and convolutions, originally arranged longitudinally, which become altered in direction by the development of a temporal lobe growing downwards and forwards, and by a change in the direction of the tentorium cerebelli from a vertical plane to one which is more nearly horizontal, so that the cerebellum is no longer posterior, but inferior in position.

The hemisphere, even in the most highly convoluted mammalian brains, is originally smooth on its surface in the embryo, and the convolutions appear and gradually assume their characteristic arrangement as the ossification of the walls of the cranial box advances. The resistance offered by the surrounding parts at last becomes so great that the growth of the cortex cerebri, and of the hemisphere generally, ceases, and the convoluted surface then exhibits the arrangement, which is characteristic of the species and of the individual.

No more striking example of a highly convoluted brain can be referred to than that of Gauss, the great mathematician, as figured by Rudolf Wagner.[1] By way of contrast, the brain of the Bushwoman figured by Mr John Marshall[2] may be looked at. In both, the plan of arrangement of the fissures and convolutions characteristic of the human brain is present; but the tortuosity and subdivision of the convolutions in the brain of Gauss contrast strongly with their comparatively simple disposition in the Bush brain. In volume Gauss's brain surpassed that of the Bushwoman, and his cranial cavity was, of course, larger; but it is not unlikely that in him the rate of brain-growth so far exceeded the rate of expansion of the cranial cavity that the resistance offered by the walls of the latter induced the complex secondary foldings on the surface of the pallium, which give to his brain its individual character.

Once a specific arrangement has become established, it is then transmitted from generation to generation by hereditary influence, so that an anatomist who has made the convolutions of the mammalian brain a subject of study can, by an inspection of the cortex cerebri, determine with tolerable precision the species to which the brain belongs. Further, the constancy of the morphological specialisation in each species points to functional differences in the areas thus differentiated from each other.

From the study of the surface of the hemisphere in the whole series of Mammalia, it is obvious that the convolutions do not exhibit a progressive and continuous development from the lower

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[1] *Morphologie des Menschlichen Gehirns*, 1860.

[2] *Phil. Trans.*, 1863.

mammals up to the higher Apes and Man. On the contrary, the brain follows apparently in each order its own plan of evolution, so that it is not uncommon to find in the same order some species with smooth brains, others possessing brains with feeble convolutions, others again with convolutions much more complicated in their arrangement. Examples of these modifications within an order have already been referred to in the Monotremata, the Marsupialia, and the Primates. The study, therefore, of the convoluted surface of the pallium in the Mammalia does not sanction the view that there has been a continuity of evolution from Ornithorhynchus to Homo in a direct longitudinal series, for well-convoluted brains may exist in an order, the general construction of the animals forming which may be inferior in other respects; whilst some species, in another order presumably higher in its organisation, may have the brain only feebly convoluted, or perhaps even with a smooth surface. This proposition may be made more clear if I give an example.

The brains of the larger Carnivora, and still more those of the Pinnipedia, have, as is well known, an elaborate arrangement of convolutions,

In the Lemuridæ, again, the convolutions are feeble, and in the Platyrrhine Marmoset the surface of the brain is practically smooth. Hence it is difficult to conceive that the brain of the Lemurs, or of the Primates, has been evolved out of the Carnivorous brain, at least after the cortex of the cerebrum in this latter order had begun to assume a convoluted arrangement. If the Primates had been evolved from the Carnivora, or even if the Lemuridæ had been derived from them, the branching off from a carnivorous stem must have occurred before the carnivorous brain became convoluted; for it is unlikely that in the process of evolution the convoluted brain could have disappeared and a smooth brain, such as we see in a Marmoset Monkey, have been its successor. The replacement of a convoluted brain by one with a smooth surface would be a retrograde or degenerative step, and not an evolution to a higher stage of development. A similar remark would also apply to the evolution of the Primates from ungulate, cetacean, or proboscidean mammals, in which the pallium had assumed a convoluted character.

As the configuration of the brain and the pattern of the convolutions have followed in each order a process of evolution characteristic of the order, the arrangement of the convolutions does not follow the same plan in the various orders. Hence in the comparison of the brains of mammals with each other, diversities of plan are recognised which make it impossible to determine the presence of precisely homologous fissures and convolutions in the whole series of the gyrencephala. There are, however, certain parts which are fundamental to both gyrencephalous and lissencephalous mammals, viz., rhinal and hippocampal fissures and a gyrus dentatus. Moreover, the area situated immediately above the corpus callosum and behind the hippocampal fissure represents in all mammals the gyrus fornicatus of the anthropotomist, which even low down in the Mammalia becomes differentiated into a distinct convolution by the formation of a splenial fissure. In each order the developmental process which determines the pattern of the cerebral cortex would seem to be regulated by the functional and physical necessities of the animals constituting the order, as well as by the conditions of hereditary descent.

The Brains of the Animals figured in this Memoir are, except figures 37, 38, 39, from original material.

Fig. 1.	*Lepus cuniculus.*
2, 22.	*Macrorhinus leoninus.*
3, 32.	*Monodon monoceros.*
4.	*Talpa europæa.*
5.	*Erinaceus europæus.*
6.	*Cynonycteris collaris.*
7.	*Pteropus medius.*
8, 9.	*Echidna hystrix.*
10.	*Phalangista vulpina.*
11.	*Macropus major.*
12.	*Macropus.*
13.	*Dasypus sexcinctus.*
14, 15.	*Cholœpus hoffmanni.*
16.	*Hyrax capensis.*
17.	*Mustela furo.*
Fig. 18.	*Felis domestica.*
19.	*Ursus maritimus.*
20, 24.	*Canis familiaris.*
21, 23.	*Trichechus rosmarus.*
25.	*Ovis aries.*
26.	*Bos taurus.*
27, 31.	*Equus caballus.*
28.	*Dicotyles torquatus.*
29, 30.	*Sus scrofa.*
33.	*Balænoptera rostrata.*
34, 40, 42.	*Homo.*
35, 41.	*Troglodytes niger.*
36.	*Hapale jacchus.*
37.	*Stenops.*
38, 39.	*Lemur nigrifrons.*

LETTERING OF FIGURES.

The Roman numerals ii. to xii., in figures 2 and 3, are the Cranial nerves from the optic to the hypoglossal.

The Arabic numerals in figures 8 and 9 are 1, 2, 3, the first, second, and third vertical transverse convolutions.

The Arabic numerals in figures 34, 35, 40, 41, 42, are as follows: 1, infero-frontal, 2, mid-frontal, 3, supero-frontal, 4, ascending frontal convolutions; 5, ascending parietal, 5′, 5″, postero-parietal convolutions; 6, angular convolution; 7, supero-, 8, mid-, 9, infero-temporo-sphenoidal convolutions; 10, supero-, 11, mid-, 12, infero-occipital convolutions; 17, marginal convolution; 18, callosal convolution; 18′, præcuneus or quadrilateral lobule; 19, hippocampal convolution; 19′, uncus or lobus hippocampi; 25, cuneus or occipital lobe. In these figures also occur the following lettering: Fr, frontal; Par, parietal; Oc, occipital; TS, temporo-sphenoidal; C, central lobe; S, Sylvian fissure; R, fissure of Rolando; I.P., intra-parietal fissure; P.O., parieto-occipital fissure; SF, IF, supero- and infero-frontal fissures; O, olfactory fissure; TR, triradiate or intraorbital fissure; A, supra-marginal or convolution of the parietal eminence; *α*, superior bridging convolution; *β*, second bridging convolution; *i*,*i*, calloso-marginal or splenial fissure; *l*,*l*, calcarine fissure; *mm*, hippocampal or dentate fissure; *nn*, collateral fissure.

In the other figures the lettering is as follows: B, olfactory bulb; Olf, olfactory peduncle; Q, quadrilateral space: V, vallecula or Sylvian fossa; H and L.H., lobus hippocampi; *ex*, external, and *in*, internal olfactory roots; *r*, rhinal fissure; *h*, hippocampal fissure; D, gyrus dentatus; S, Sylvian fissure; *cr*, crucial fissure; *ps*, præ-sylvian fissure; *co*, coronal fissure; *ml*, medilateral fissure; *l*, lateral fissure; *ss*, supra-sylvian fissure; *ssp*, posterior part of supra-sylvian fissure; *pr*, posterior part of rhinal fissure; *f* and *fr*, frontal fissures; *ip*, intraparietal fissure; *p*, parallel fissure; *ca*, calcarine fissure; *col* and *cl*, collateral fissure; *io*, intraorbital fissure; *ol*, olfactory fissure; *sp*, splenial fissure; *g*, genual fissure; *ssp*, suprasplenial fissure; *ph*, postero-horizontal fissure; *psp*, postsplenial fissure; *isc* and *esc*, internal and external supraorbital convolutions; *sac* and *m*, sagittal or marginal convolution; *mlc*, medilateral convolution; *ss* and *ssc*, supra-sylvian convolution; *sc* and *syc*, Sylvian convolution; *sg* and *sgc*, sigmoid convolution; *cc*, callosal convolution; *spc*, splenial convolution; *sspc*, suprasplenial convolution; P, pituitary body or hypophysis cerebri; CS, corpus striatum; OT, optic thalamus; C_1, 1st cervical nerve.

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