The Mammalian Cerebral Cortex, with Special Reference to its Comparative Histology. I. Order Insectivora.—Preliminary Communication.

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The results and conclusions brought forward in this paper form a portion of the outcome of an extensive investigation dealing with the cortex cerebri in various orders of mammals. The work has special reference to the neopallium only, and has for its prime purpose an endeavour to shed some further light upon the functional significance of the cerebral cortical lamination.

Animals Examined and Methods of Study.

The brains of the animals belonging to this order examined are :—

1. The Mole (*Talpa Europea*). 2. The Shrew (*Sorex vulgaris*). 3. The Hedgehog (*Erinaceus Europeus*).

The cerebral cortex has been examined by means of complete series of sections cut in almost every possible direction and stained by one or other modification of the Nissl method.

As part of the method of study throughout the entire investigation, the natural habits of the animals examined, and their educability, as far as facts relating to the latter are available, have been considered when attempting to correlate structure and function.

Macroscopic Appearances and Microscopic Furrows.

All are almost smooth highly macrosmatic brains. That of the Hedgehog is one of the simplest mammalian brains. It presents in addition to the rhinal fissure a short presylvian furrow; the latter is not found macroscopically in the Mole and Shrew, but is seen on microscopic examination of sections. By this method also, in the Mole only, two shallow more or less longitudinal curved furrows can be traced on the dorso-lateral aspect of the hemisphere, which appear to represent foreshadowings of the corono-lateral and supra-sylvian sulci.

Signs of greater differentiation of the neopallium of the Mole, as compared with the Hedgehog especially, are further exhibited on microscopic examination of the structure of the cortex. The optic nerves in the Mole and

Shrew are reduced to small threads. In the Hedgehog these nerves are considerably larger. In all three the fifth nerves are relatively very large.

The Lamination of the Neopallium.

General Remarks.—The classification of the cortical layers adopted by the writer is that introduced by J. Shaw Bolton. The latter considers that the human cerebral cortex is constructed upon a five-layered type—viz., I, Molecular; II, Pyramidal; III, Granular; IV, Inner line of Baillarger; V, Polymorphic. Of these only three are primarily cell layers—viz., the pyramidal, granular, and polymorphic, Layers I and IV being primarily fibre layers, although containing nerve cells—the cells of Cajal in Layer I, and the Betz cells (psycho-motor region) or solitary cells of Meynert (other regions) in Layer IV. The outstanding features of this classification are: (1) The recognition of the granular layer as separating the true pyramidal *layer* above from the more or less pyramidal *shaped* cells which may be found below this layer, for the cells of Layer IV are not "pyramidal" cells at all, the Betz cells in the psycho-motor area constituting "the origin of the important tract for skilled voluntary movement," whilst the solitary cells of Meynert in other regions "probably possess a somewhat analogous function." (2) The consideration of the pyramidal layer as forming *one* layer developmentally and functionally.

Bolton, as the result of his studies of the development of the human cerebral cortical layers, and of their depth in the normal individual as well as in various degrees of amentia and dementia, has come to the following conclusions as to the functions of the three primary cell layers. The pyramidal layer "subserves the psychic or associational functions of the cerebrum." The granule layer "probably subserves the reception or immediate transformation of afferent impressions, whether from the sense organs or from other parts of the cerebrum," whilst the fifth, or polymorphic layer, "probably subserves the lower voluntary functions of the animal economy."

When dealing with the mammalian cortex generally one or two further explanations are necessary.

The term "granular" is used in a wide generic sense and as indicative of a certain cortical layer rather than of the cell constituents of this layer, which latter, in an adult animal, may take the form of angular, quadrilateral, stellate or even small pyramidal-shaped cells, or a mixture of these elements. In some regions of the cortex in certain animals these elements of the granular layer may be scattered and comparatively few in number; yet their recognition is of importance, for such provides the means by which the lower limits of the true pyramidal layer may be determined. Owing

to the difficulty experienced in accurately separating the fourth and fifth layers (which tend to intermingle) in the cortex of some animals, the writer prefers to speak of these layers together as *infra-granular*. It is also proposed for the sake of definiteness to term the true pyramidal layer (*i.e.*, Layer II) the *supra-granular* layer.

Areas in the Neopallium.

The appearances of the cortex in the Mole and Shrew being very similar, the following, concerning the cortex of the Mole, may be taken as applying also to the Shrew excepting when the latter is specially mentioned:—

1. *Dorso-lateral Surface.*—In the Mole this region presents two main and distinct types of cortical structure, with certain areas of comparatively undifferentiated cortex (fig. 1).

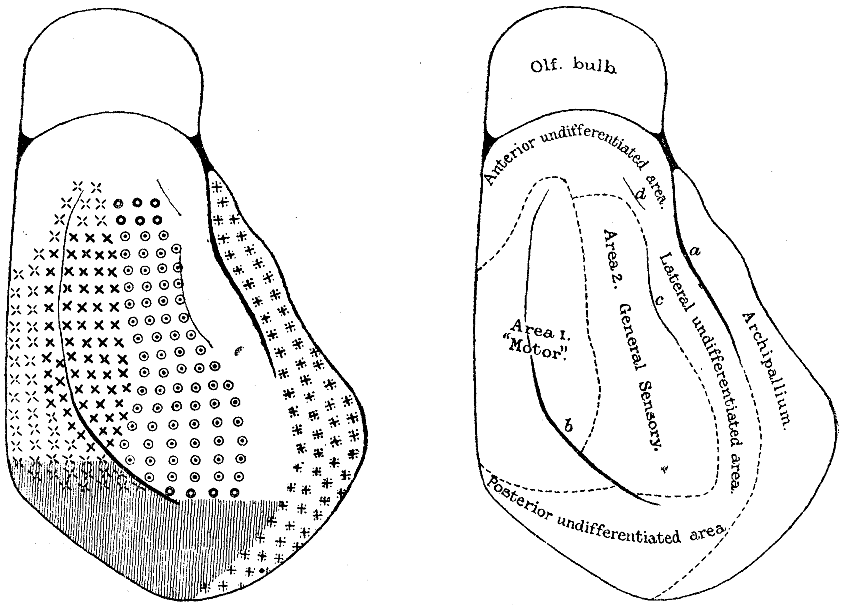

FIG. 1.—Dorso-lateral view of the Right Hemisphere of the Mole.

Left-hand figure. × Area 1, "Motor"; ⁙ the same, but less characteristic; ⊙ Area 2, General Sensory; ◎ the same, but less characteristic; ⁜ Archipallium.

The anterior, lateral, and posterior areas of undifferentiated cortex are left blank excepting the portion of neopallium represented as shaded, which is thinner than the remainder.

Right-hand figure. *a*, rhinal fissure; *b*, *c*, and *d*, probable representatives respectively of the corono-lateral, supra sylvian, and presylvian sulci; *b*, *c*, and *d*, vary much in individual distinctness in different hemispheres. The figure is a composite one.

Area I: Motor.—This extends antero-posteriorly from a short distance

behind the anterior pole to about the posterior quarter of the hemisphere, and laterally from the dorso-mesial margin (or more or less close to this anteriorly and overlapping this posteriorly), to about half-way between the dorso-mesial edge and the rhinal fissure, the lateral limits varying somewhat at different points (figs. 1 and 2).

Area II: General Sensory.—This occupies an extensive region lateral to Area I, but does not reach as far as the rhinal fissure, being separated from the latter by a zone of undifferentiated cortex (fig. 1).

The features of Area I are less characteristic mesially, anteriorly and posteriorly, and of Area II anteriorly and posteriorly. These two fields appear in every way to be the best developed areas of the neopallium and to be amongst the oldest phylogenetically. Owing to their different histological appearances, Areas I and II in the Mole can be readily delimited. From the relatively greater numbers and prominence of the large cells (homologues of Betz cells) in Layer IV, it is concluded that Area I possesses especially motor attributes, and that on account of the greater development of the granular layer throughout Area II, the latter

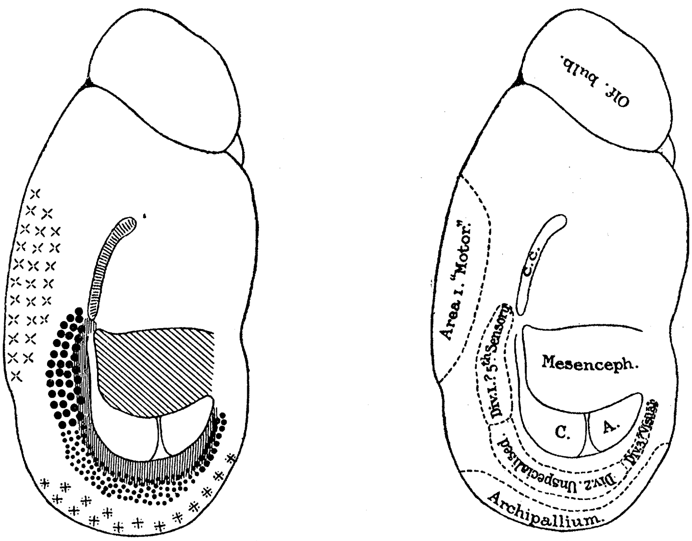

FIG. 2.—Postero-mesial aspect of the Left Hemisphere of the Mole, to illustrate especially the position and relations of the postero-mesial region of cortex characterised by a well-marked granular layer. The right-hand figure is explanatory of that on the left.

is sensory in function. It is also thought that probably Area II is largely concerned with kinæsthetic impressions, these appearing to constitute a considerable part of the basis of such intelligence as these animals possess.

In the Hedgehog, although interpretation of the cortical structure is much

more difficult than in the Mole, a similar large field of comparatively well-developed cortex can be distinguished on the dorso-lateral and mesial aspects, occupying the same relative position and being of about the same relative size, as are Areas I and II taken together in the Mole. No satisfactory criteria, however, have been found from cell lamination alone by the aid of which this region can be divided into Areas I and II as in the Mole. Hence, it is considered that although there may be some attempt at differentiation of these areas in the Hedgehog, it is probably more correct to regard the entire field in the latter as a combined sensori-motor area.

The explanation which suggests itself of these structural differences is that they stand in relation to the fact that the Mole and Shrew are possessed of more numerous and better motor accomplishments than the Hedgehog, and so the former have a more specialised zone of "motor" cortex, the latter being a comparatively lethargic animal, and dependent for its survival rather upon its protective armour of spines than upon its activity.

Areas of Undifferentiated Cortex.—In the anterior (extending also to the mesial), lateral, and posterior portions of the neopallium are three fields of moderate size in all three animals, to which, from the want of any special feature in their lamination, no attempt is made at the present time to attach any peculiar functional value. They are regarded as indifferent or unspecialised regions of cortex.

The area of the cortical distribution of the eighth nerve has not been definitely localised. By analogy one would expect to find this probably in about the middle and towards the anterior part of the outer portions of the field termed Area II in the Mole, or just external to this, and in the corresponding region in the Hedgehog.

2. *Anterior Surface.*—Occupying almost the whole of the anterior and inferior aspect of the frontal pole and curving forwards to join the olfactory bulb, is a small area of comparatively well-developed cortex, sharply marked off from the less differentiated cortex posteriorly. This is of about the same relative size in the Mole and Hedgehog, and probably constitutes a neopallial representation of the olfactory sense.

3. *Mesial Surface.*—This may be divided into (1) the straight anterior portion, and (2) the curved postero-ventral portion which arches over and round the mesencephalon and hippocampus (figs. 2 and 3).

(1) The straight portion presents anteriorly an area of undifferentiated cortex continuous with that on the dorsal aspect, posteriorly a field with modified motor characters joining that in the dorsal surface, and between these an area with some indefinite sensory characters. Similar areas are seen in the Hedgehog.

(2) The more definite lamination (figs. 2 and 3) occupies the remainder of the posterior part of the straight mesial surface and a large part of the curved postero-mesial and ventral surfaces. This region, from sections taken in various directions, was found to be distinguished by an exceedingly definite granular layer, and it appears to be a portion of neopallium inserted as a curved tongue between the mesial portion of Area I (in

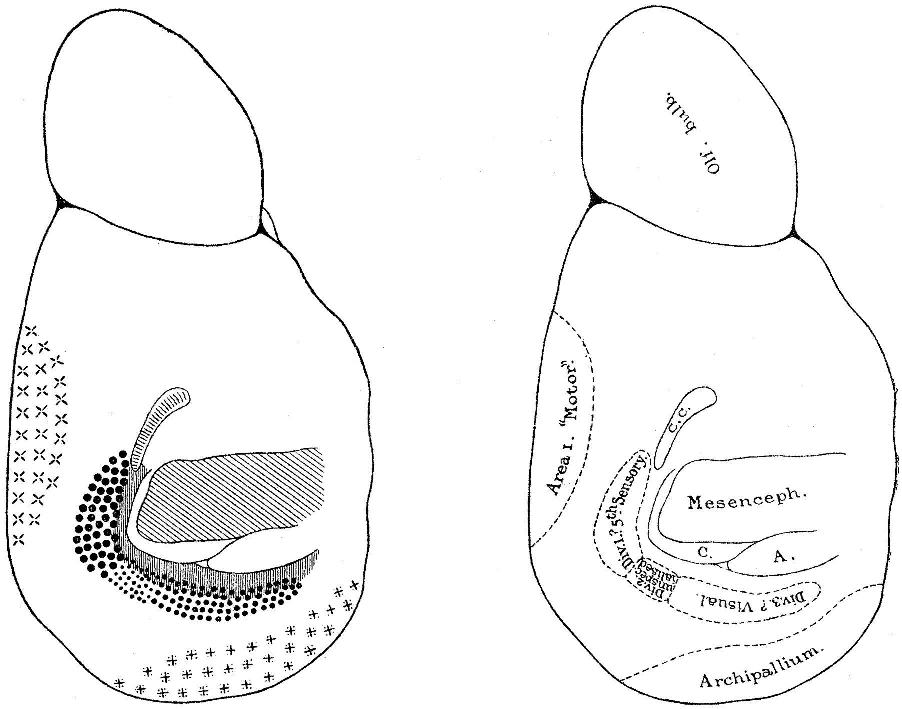

Fig. 3.—Postero-mesial aspect of the Left Hemisphere of the Hedgehog, for comparison with fig. 2 (Mole).

Mole) and the cortex behind and below this, including archipallium on the one hand, and the posterior part of the corpus callosum and hippocampus on the other. The area is not of the same shape in the Mole as in the Hedgehog, owing to the hemisphere being moulded in a different way in the two animals. This region, although characterised throughout by the well-marked granular layer referred to, presents certain differences of detail, owing to which it has been separated into three divisions in each animal. The anterior and superior portion (Division 1) is of about the same relative size in the Mole as in the Hedgehog. In both there are good granular and infra-granular layers, and in the Hedgehog a shallow but definite supra-granular layer. The middle portion (Division 2) is relatively

larger in the Mole than in the Hedgehog, but in both, comparatively to Divisions 1 and 3, it presents unspecialised features. The inferior portion (Division 3) is relatively not only considerably larger in the Hedgehog than in the Mole, but in the former it is a more histologically distinct field, showing not only a well-formed "granular" layer (the cellular elements in which, however, are mostly angular or small pyramidal in shape), but a comparatively good infra-granular and a definite, though shallow, supra-granular layer. In the Shrew this division is rather better developed than in the Mole.

Owing to the presence throughout this region of such a deep and definite granular layer, it is concluded that this field is sensory in function, and regarding it the following suggestions are made :—

(*a*) The area is much too large to be concerned only with the cortical distribution of the optic nerves, which are relatively so minute in these animals, especially in the Mole.

(*b*) The inferior portion (Division 3) only is visual. In the Mole this portion is a mere vestige; in the Hedgehog it is better developed and relatively larger, having apparently extended upwards somewhat and encroached upon the area of unspecialised granular cortex (Division 2) as compared with the Mole.

(*c*) The middle and superior portions (Divisions 2 and 1) may correspond to the large infra-calcarine area of certain relatively higher mammals (*e.g.*, Ungulata and Carnivora), in which, owing to the greater development of the visual faculty, the inferior portion (Division 3, visual) has, so to speak, extended upwards, backwards, outwards, and forwards so as to overlie the middle and superior portions, and has become the calcarine region.

(*d*) The relatively well-developed superior and anterior portion (Division 1) of the two specialised divisions in both Mole and Hedgehog may be concerned with the cortical distribution of the fifth sensory nerve. On account of the importance of the fifth sensory nerve as an avenue of information to these mammals through snout or vibrissæ touch, or both, and, in view of the large size in them of the fifth nerve, it seems probable that the sensory portion of this nerve should have a very special cortical representation.

The Cerebral Cortical Layers. (Neopallium.)

Although the total depth of the cortex in the best developed regions is different in the Mole, Shrew, and Hedgehog, the relative depth of the separate layers, supra- and infra-granular particularly, appears to be about the same in all. The following micrometric measurements of the cortical layers in three areas of the Mole's cortex, which have been kindly furnished

by Dr. J. S. Bolton, may be taken as fairly typical also of the relative differences in depth of the supra- and infra-granular layers especially, in the corresponding regions in the other two animals.

Micrometric Measurements of the Cortex of the Mole.*

	Area 1.—Motor (average of 23).		Area 2.—General sensory (average of 17).		Lateral area (average of 7).	
	mm.	mm.	mm.	mm.	mm.	mm.
Layer I.—Molecular	0·162		0·144		0·095	
" II.—Supra-granular	0·092	0·320	0·093	0·367	0·095	0·320
" III.—Granular	0·228		0·274		0·225	
" IV.—Infra-granular	0·147	0·304	0·176	0·377	Not separated	0·471
" V.	0·157		0·201			
Total	0·786 mm.		0·888 mm.		0·886 mm.	

It will be observed that in Area I the supra-granular layer (II) is less than one-third the depth of the infra-granular layer (IV and V), and that in Area II it is only about one-quarter of the depth of the latter. If Layers II and III (supra-granular and granular) are taken together they only approximately equal in depth the infra-granular.

A very abbreviated comparative summary of these measurements in the case of the Mole, and those of Bolton† from the prefrontal cortex in the sixth month's human fœtus, the full-time new-born child and the normal human adult, reveals the following facts, shown approximately in fig. 4:—

(1) The granular layer is of approximately the same depth in the Mole (Areas I and II) as in the normal human adult prefontal cortex.

(2) The supra-granular (pyramidal) layer: (*a*) in the sixth month's human fœtus is nearly two and a-half times the depth of that of the Mole (Areas I and II); (*b*) in the full-time child it is five to six times the depth of that of the Mole; (*c*) in the normal human adult nine times the depth.

(3) The infra-granular layer.—In the sixth month's fœtus and full-time

* With regard to the lateral area of undifferentiated cortex, the cellular elements in which are comparatively unspecialised, it is obvious that its increase in depth as compared with Area I is due chiefly to the infra-granular layers (IV and V), the portion of the cortex from which the measurements were taken being in the neighbourhood of the rhinal fissure, and so forming what would correspond to the apex of a convolution.

† Bolton's observations as to the ontogenetic development of the cerebral cortical layers have been confirmed by the writer in the cases of a fourth, sixth, and eighth month human fœtus, and the same relative order of development of the layers has been found by him to hold good with regard to several fœtal and new-born lower mammals belonging to different orders.

child the combined fourth and fifth layers are little over the depth of those layers in the Mole. In the normal human adult these combined layers are only a little over half as deep again as in the Mole (1·56 to 1).

The increase in depth of the human cortex cerebri as compared with that of the Mole is therefore *very* largely due to increase in the supra-granular layer.

Conclusions as to the Functional Significance of the Supra-Granular and Infra-Granular Cortical Layers.

Bolton's views as to the functional value of these layers have already been briefly stated (p. 151). The following conclusions, which apply only to mammals, form a complement of them from the point of view of the Insectivora and of the lower mammals belonging to various other natural orders so far examined.

1. The infra-granular layer (IV and V) (omitting the constituent cells which possess motor or analogous functions), which is relatively so fully developed at birth, is concerned especially with the associations necessary for the performance of the instinctive activities, that is, all those which are innate and require no experience or education. These involve many complex actions, such as the seeking appropriate shelter and protection (*e.g.*, tunnelling of Mole), the hunting for food—each after his own kind—and the quest of the opposite sex. Such more or less stereotyped activities may show signs of improvement, firstly as the result of the perfection by use of an inherited mechanism, and secondly as the result of the intermingling of activities for which it is concluded that the supra-granular layer is responsible. In the latter case, however, the activities would merge into those which are more properly described as habitual intelligent or into the class of incomplete instincts (Lloyd Morgan), or mixed instincts (Romanes).

2. The supra-granular (pyramidal) layer subserves the higher associations, the capacity for which is shown by the educability of the animal. It has therefore to do with all those activities which it is obvious that the animal has acquired by individual experience, and with all the possible modifications of behaviour which may arise in relation to some novel situation, hence with what is usually described as indicating intelligent as apart from instinctive acts.

In practical animal behaviour the two sets of processes are probably more or less constantly interwoven, the higher activities (supra-granular layer) coming to the aid of the lower as far as the capability of the animal allows. In the case of the lower mammals (*e.g.*, Insectivora) the limits of this capability are comparatively soon reached, and, correspondingly, these

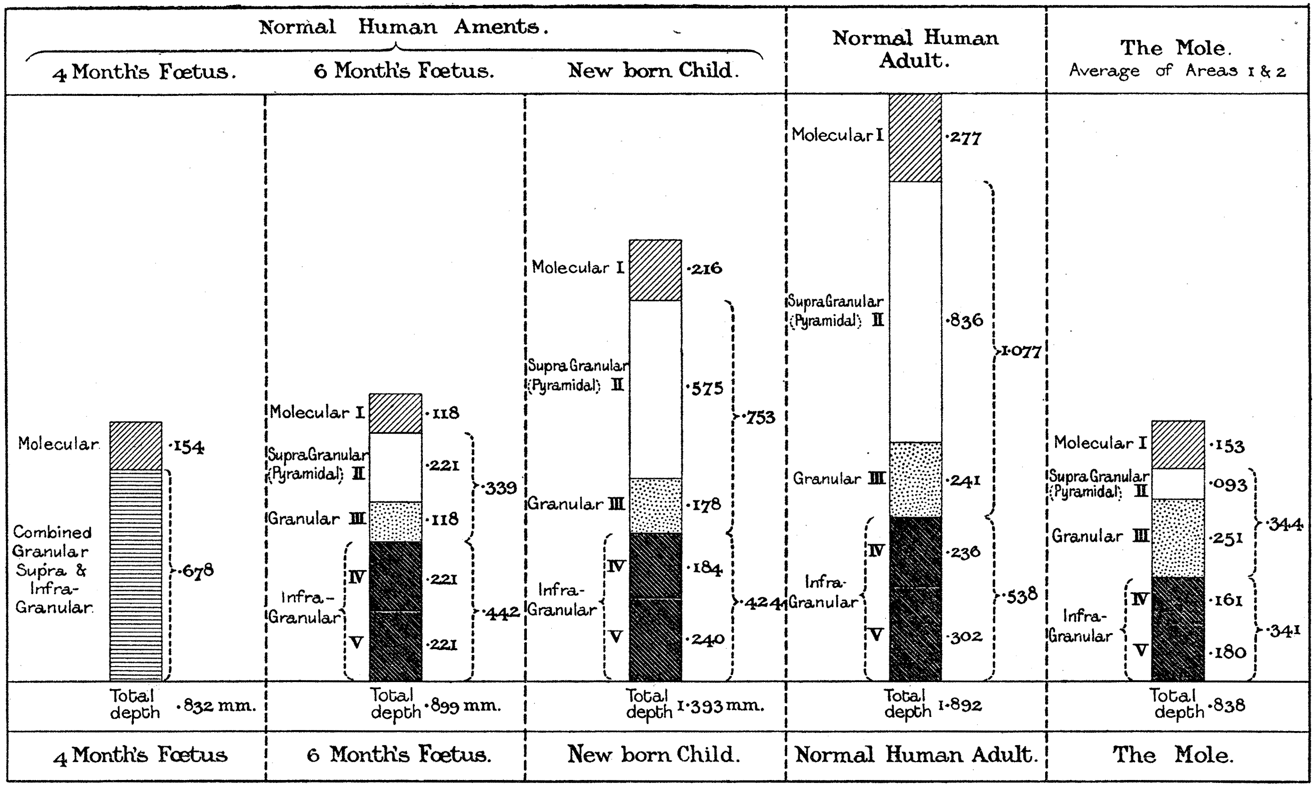

Fig. 4.—Illustrates approximately the relative depths of the Cerebral Cortical Layers in normal Human Aments (4 and 6 months' fœtus and new born child), the normal Human Adult and the Mole.

The micrometric measurements in the first four cases are taken from "The Histological Basis of Amentia and Dementia" ('Archiv of Neurology,' vol. 2, 1903) by J. Shaw Bolton; those of the cortex of the Mole are also by Dr. Bolton. Supra-granular (pyramidal) layer left blank; infragranular (IV and V) shaded darkly.

mammals possess a relatively poor supra-granular layer. Many of these lower mammals have adopted a safe mode of life, others have resorted to fecundity. With these, which may for present purposes be termed extraneous aids to survival, their essentially instinctive activities have been relatively sufficient to ensure their continued existence. There has therefore in these mammals been little necessity for the development of a supra-granular layer, the infra-granular providing most of the necessary cortical physical basis required for practical behaviour.

The infra-granular layer, with the reservation to which reference has been made, thus constitutes the earlier developed and more fundamental associational system of the cerebral cortex; the supra-granular, a higher and accessory system, super-added, and of any considerable functional importance only in certain regions in lower mammals such as the Insectivora.

In view of the above conclusions, attention may be briefly directed to the following points. Areas I and II—motor and general sensory—in the Mole and Shrew (and the combined field in the Hedgehog) appear in every sense to be the most completely developed regions of neopallium which these animals possess, and are the only areas in the two former animals having a supra-granular layer of any considerable depth and complexity as regards its individual cell elements. In the Hedgehog, in the area which is believed to have visual functions, there is as regards individual cells a moderately well-developed, though thin, supra-granular layer, whilst this is practically absent in the comparatively blind Mole and Shrew in the analogous region.

Note to FIG. 4.—The infra-granular layer in the 6-months' fœtus and new-born child were practically of the same depth in the specimens measured, viz., ·442 to ·424. In the figure the darkly-shaded part (infra-granular layer) in the third column is therefore represented somewhat too deep.