

Part II.

The principles of comparative field organisation in the cerebral cortex.

As a result of the observations described in Part I we are now in a position to divide the cerebral cortex into structurally circumscribed regions, in other words to construct a histological topographic map of the surface of the hemispheres.

We demonstrated above that modifications of cortical architecture often involve the whole depth of the cortex at a given locus on the surface and that such modifications frequently take place abruptly and quickly, resulting in relatively sharp borders between neighbouring structural regions. As an example, Figure 80 represents a coronal section of the hemisphere of a cat through the middle of the coronal sulcus and reveals several cortical structural types, and their borders, lying in a single plane. Figure 81 shows similar, even sharper, transitions at the borders of the calcarine cortex in a coronal section of the occipital lobe of a monkey. Finally, in Figure 82 the transitions from the hippocampus to the subiculum, presubiculum, entorhinal area and perirhinal area in that order are shown for a marsupial, the wallaby.

We likewise learned that sudden transitions between different cortical types exist in all mammalian orders, often just as dramatically in lower species (such as the kangaroo and rabbit) as in man, and that certain forms of regional modification of lamination that are found in man are also identifiable in essence throughout the whole mammalian class, although more or less modified in individual species (Figures 20 to 22, 24 to 26, 58 to 63, 64 to 67, 68 to 77).

These facts form the point of departure for the establishment and spatial demarcation of homologous cortical fields, that is those with similar histologi-

cal cellular structure - the cytoarchitectonic areas - in different mammalian orders and so provide the foundations of a **comparative surface parcellation of the cerebral cortex**.

It will thus be our task in Part II to determine the specific forms of field structure in individual animals and so establish common features and variations in the arrangement of fields in different animals. Only in this way will common aspects of comparative localisation emerge. The problem of comparative cortical topography can thus be reduced to the following questions:

1. Is there a homology or merely a certain similarity in the topographic field organisation in different mammalian orders; in other words is the cortex made up of homologous structural regions based on common rules throughout the whole mammalian class or must one assume a special topographical structural principle for each species or at least each major animal group?

2. What are in general the common features and variations in the cortical parcellation of different species?

3. Are there constant and inconstant fields and how do the former vary in form, size and place in individual families or species?

Before we enter into a major discussion of the questions thus posed we should make a few remarks about the material and the brain maps.

As to the material, it is evident that a study that is only intended as an initial general basis for a discipline cannot extend to the whole zoological system nor even to all orders of a class, let alone to the majority of families or species.

To obtain an exhaustive topographic division of the cortex in a single species necessitates the production of several uninterrupted series of sections through the whole cerebral hemisphere and their comparative study, work that, apart from its interpretive difficulties, is technically extraordinarily time-consuming and tedious. Such a study must be limited initially to a few major animal groups, or a small number of representatives of each, for the purpose of orientation. As a preliminary I have determined the field distribution in the cortex of representatives of seven orders, namely

1. primates by man, several cercopithecids and marmosets,
2. prosimians (*96) by the lemur and mouse lemur,
3. chiropterans by the flying fox (*97)
4. carnivores by the kinkajou (and partially the dog),
5. rodents by the rabbit (*98), the ground squirrel and partially the mouse,
6. insectivores by the hedgehog,
7. marsupials by the kangaroo and possum.

I can present finished brain maps of man, guenon, marmoset, flying fox, kinkajou, rabbit, ground squirrel and hedgehog. In addition I have taken limited samples from many other animals and animal groups (orang-utan, capuchin monkey, indris, mouse lemur, pipistrelle, cat, weasel, opossum, echidna and others) but have not yet completed a definitive cortical localisational study of the whole hemisphere.

This material is certainly not exhaustive, but it permits the establishment of the principal common features in the overall organisation of the cortex of

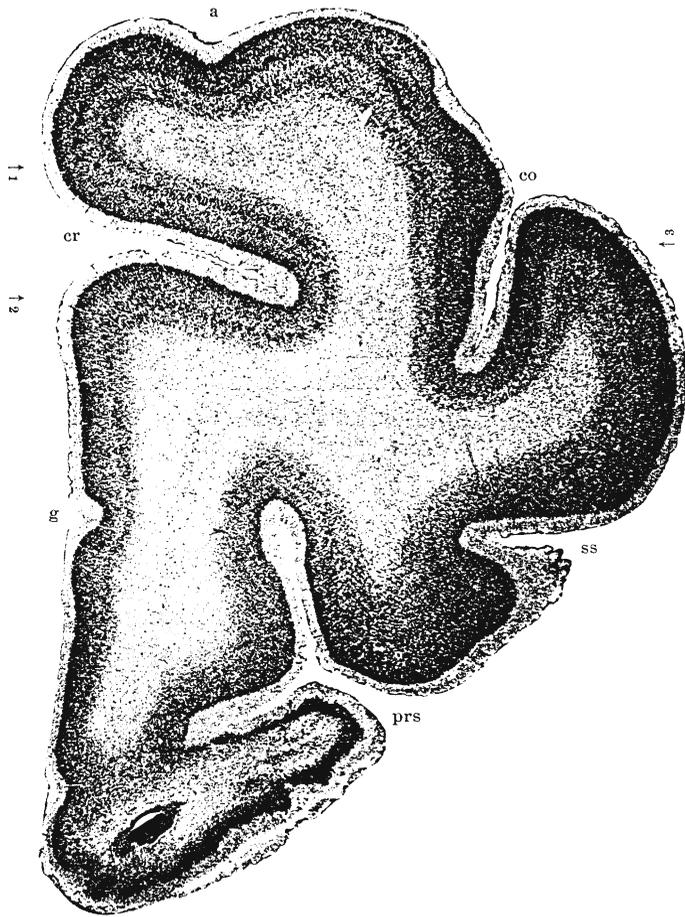


Fig. 80. Coronal section through the hemisphere of a 14-day-old cat (*Felis domestica*). Transition of the basic six-layered cortex to the agranular giant pyramidal cortex (at ↑1) on one side and to the granular frontal cortex (↑3) on the other. On the medial side is the precingulate cortex (↑2). a = ansate sulcus, cr = cruciate sulcus, co = coronal sulcus, ss = suprasylvian sulcus, prs = presylvian sulcus, g = genual sulcus.

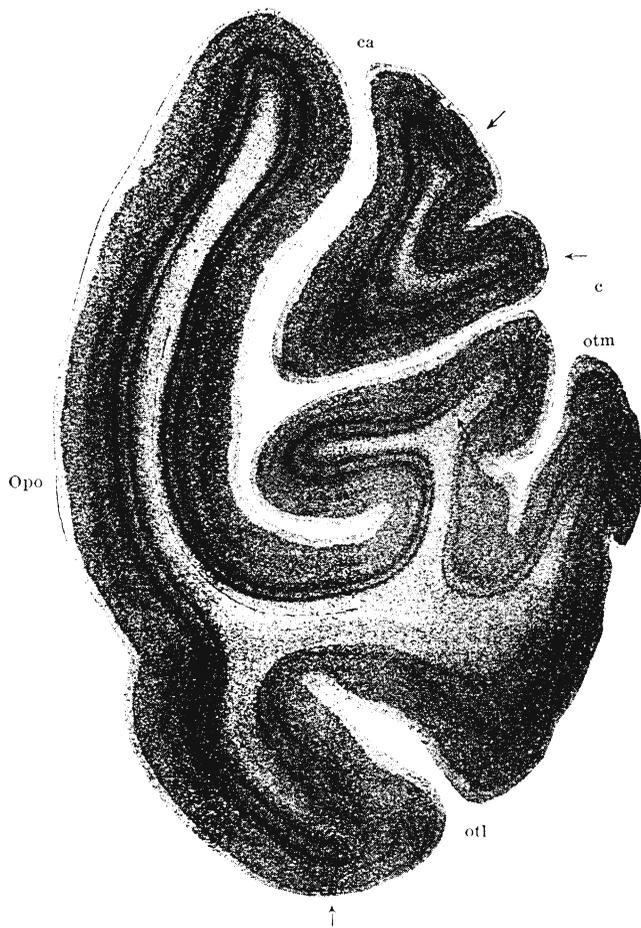


Fig. 81. Coronal section through the occipital region of a monkey (*Macacus rhesus*). There are four transitions from calcarine cortex to adjacent cortex. A diminution in the number of layers is clearly visible at the arrows. c = main stem of the calcarine sulcus. ca = ascending ramus of this sulcus. otm = medial occipitotemporal sulcus. otl = lateral occipitotemporal sulcus. Opo = occipital operculum.



Fig. 82. Coronal section through the piriform lobe of the wallaby (*Onychogale frenata*) with several abrupt architectonic transitions.

various mammals as well as the detection of certain special particularities in the cortical organisation of individual orders or families. This suffices for the object of the present investigation that simply aims to elucidate the basic principles of the comparative subdivision of the cortex. The description of special peculiarities for each individual species must remain the task of later detailed study.

With regard to the brain map, one should note that the individual structural fields are marked with various diacritical symbols on the lateral and medial surfaces of the hemispheres of each brain studied. Homologous cortical types or areas have, in general, received identical symbols in the different animals, but the same symbols do not always indicate absolute homologies, for often one can only speak of partial or relative homologies. When there is superimposition or fusion of several adjacent fields in a given animal, which are separate in others, this is indicated in the brain maps by mixing and superimposition of the corresponding symbols. The reproach has been raised from various quarters, although it seems to me not always with sufficient knowledge of the facts and also often without adequate grasp of the pertinent work, that such brain maps give a false picture of the true relationships and inspire erroneous localisational concepts by drawing sharp borders where there are none and by spatially segregating structural regions that should not be absolutely separated. One may reply that a brain map, being essentially like any schematic representation, necessarily implies certain distortions. I have pointed this out whenever the opportunity arose in my earlier publications, emphasising particularly the difficulties of the graphic representation of surface

subdivisions in a convoluted hemisphere. A surface view must represent fields and borders that lie in the depths of sulci or on buried gyri; furthermore it must project curved areas on a flat surface which will result both in distortions of perspective and in spatial displacements. In addition, transitions between neighbouring fields often do not produce truly sharp borders, but are gradual, whereas the map must always draw a boundary if it is to represent topical relationships. Thus certain inaccuracies must be admitted, as in any diagram. In spite of this, the brain maps present the true position and mutual relations of fields and anyone can use them beneficially in comparative studies as long as they do not seek more from them than is intended, that is to serve as aids to orientation.

We shall proceed with the following descriptions by first considering the features of cortical field subdivision in a series of individual animals by means of the brain maps, and then debate more general questions in the following chapters. We shall begin with man and continue progressively down the mammalian class.