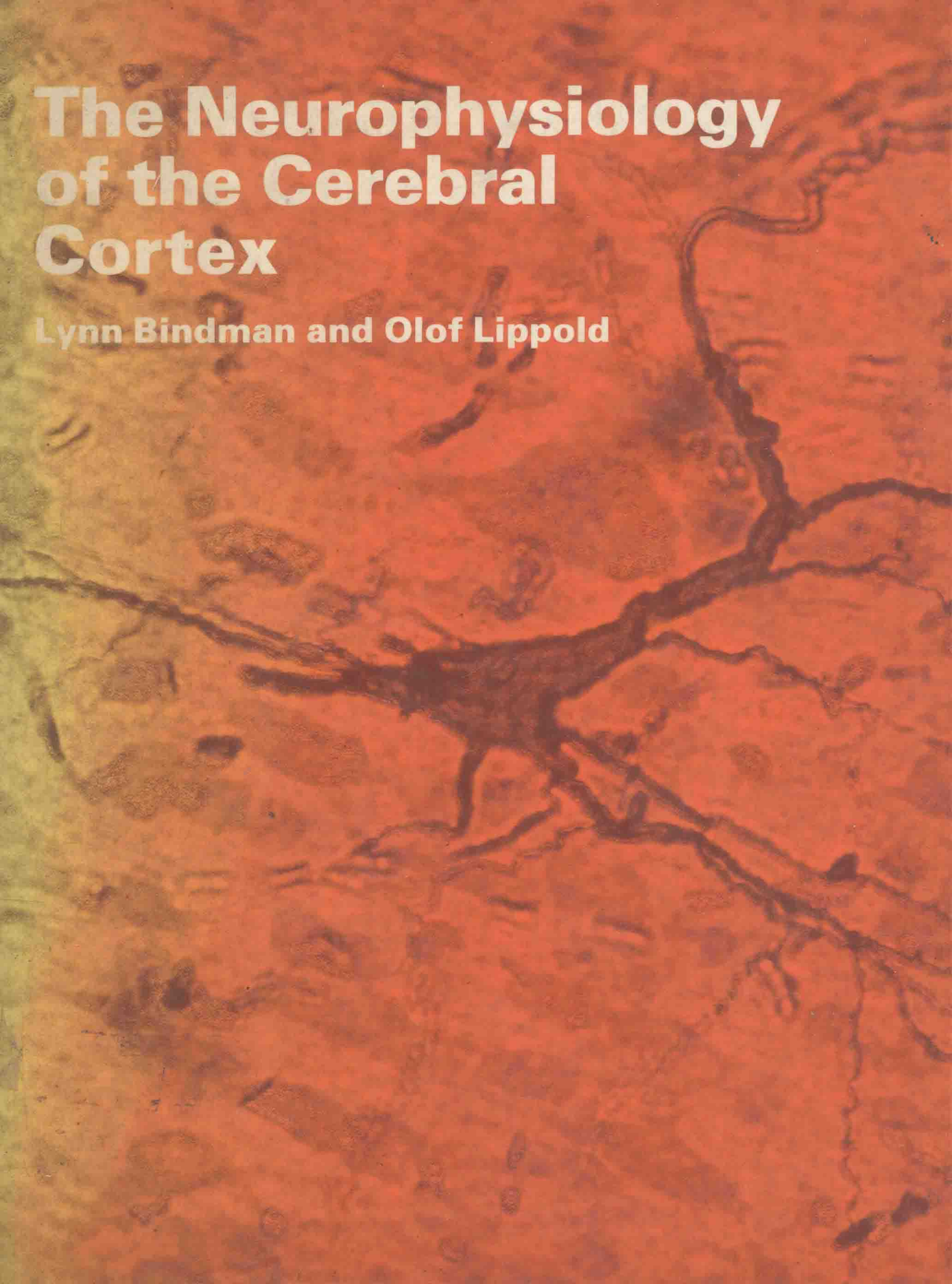
The Neurophysiology of the Cerebral Cortex

Lynn Bindman and Olof Lippold



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Preface

As a result of the challenge involved in teaching advanced students about the cerebral cortex, we became aware of the difficulties that these students have in finding simple and yet suitably critical accounts of the subject. Teaching a subject such as neurophysiology is a dynamic process which involves considerable interaction between teacher and student. One is forced to become critical of much of the material forming the basis of the subject, sometimes because the evidence is insecurely founded, sometimes because dubious assumptions masquerade as proven facts. There is a pressing need, both for a more general source of information and for help in the interpretation of the voluminous, and not always obviously relevant, literature in the field.

This book is intended for readers who want an account of the present state of knowledge of the cerebral cortex, given in more detail than in most textbooks on the central nervous system. It will provide information for research workers as well as for undergraduate and graduate students of physiology and medicine. As authors we were faced with the choice of writing it ourselves or co-opting experts to write individual chapters. The latter course might well have resulted in more penetrating assessments of specialist fields, but in our view the book would then have suffered from the disadvantage of being yet one more collection of unrelated review articles. We were concerned to provide a coherent account of the background to the research on the neurophysiology of the cerebral cortex thus enabling the reader to understand current reviews and original papers. The level is therefore somewhere between that of the review article and a standard textbook; we have aimed to provide a more detailed and more critical appraisal than is found in the latter. With just two authors tackling such a large topic, there is inevitably some inequality of emphasis in the subject matter, reflecting our own interests and knowledge. We have tried to mitigate these disadvantages by asking experts to read various chapters and by providing references to other books and reviews where appropriate.

London, 1980

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Acknowledgements

We would like to thank many people whose help contributed to this book.

Professor Don Kennedy of Stanford University read the entire text as each chapter was written. His criticisms and comments were invariably justified and helpful, and greatly improved the quality of our efforts.

Earlier versions of individual chapters were subjected to the scrutiny of various colleagues at University College London, and we thank them most warmly for their useful corrections and suggestions. Professor Keith Webster (now at King's College London) read Chapters 2, 3 and 10; Dr Judy Trott (now at Bristol University) commented on Chapter 8; Professor Mike Bradbury (now also at King's College London), whose excellent book on the cerebro-spinal fluid has now appeared, helped us with Chapter 9; and Dr Pete Ellaway with Chapter 14. We should like to thank Dr Semir Zeki in particular, not only for his helpful criticisms of Chapter 11, but also for his advice with regard to the selection of material on the visual cortex.

Dr Trevor Stone (of St George's Medical School) and an anonymous reviewer read the finished typescript, and made many useful points.

Apart from our scientific colleagues, a number of people gave us invaluable assistance. The artwork was done by Mrs Audrey Besterman, who made many creative alterations and improvements to our rough sketches. The typing was done with superb accuracy and speed by Mrs Kathleen Wilder, and Miss Penny Alderson has given us intelligent secretarial help. Mr Arly Winton put in many hours of painstaking work, checking the text against the reference list, checking the references themselves and arranging the alphabetical list of references. Dr Barbara Cogdell compiled the index. We should like to thank the editorial staff at Edward Arnold for their careful work on the book. In addition Lynn Bindman would like to acknowledge the help her family have provided. Her parents Nettie and Arly Winton, her husband Geoffrey, and children, Jonathan, Daniel and Miriam, have looked after one another so well that she was free to work relatively undisturbed.

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General introduction: the mammalian brain

1.1 The mammalian brain

Through the ages men have wanted to understand their own brains, both in terms of structure and function. Twenty-five centuries ago, Hippocrates wrote:

> 'Men ought to know that from nothing else but the brain comes joys, delights, laughter and sports, and sorrows, griefs, despondency and lamentations. And by this, in an especial manner, we acquire wisdom and knowledge, and see and hear, and know what are foul and what are fair, what are bad and what are good, what are sweet and what unsavoury; some we perceive by habit and some we perceive by utility.... And by the same organ we become mad and delirious, and fears and terrors assail us, some by night and some by day, and dreams and untimely wanderings, and cares that are not suitable, and ignorance of present circumstances, desuetude and unskilfulness. All these things we endure from the brain.'

Over the past century the scientific investigation of the brain has uncovered a wealth of information, so that we now have some understanding of how sensory functions, such as seeing and hearing, are carried out by parts of the brain. How we acquire wisdom and knowledge is a fascinating but much harder problem to study. The largest part of the brain in Man is the cerebral cortex, and this book is restricted to an account of its neurophysiology. It is an artificial separation from the study of how the brain works as a whole, because cortical function both determines and is affected by activity in other parts of the brain, and indeed in the whole body. Sensory nerves relay information from the periphery of the body to the spinal cord and thence to the brain; motor nerves coming from the brain send instructions to control the activity of muscles and glands. Some of the motor activity is purely reflex, some is modified by the action of the brain. The brain can also affect and control bodily functions by means of endocrine secretions. The brain coordinates and controls bodily functions to modify the responses of the animal in accordance with present needs and past experience.

Since we shall be referring to many parts of the brain other than the cerebral cortex we shall begin with a brief description of the structure of the brain as a whole and of the main functions of the component parts.

Structure of the brain

The brain is composed of nerve cells (neurones), supporting cells (neuroglia), blood vessels and various membranes. Estimates are that the average human brain contains at least 10^{11} neurones, all laid down before birth and irreplaceable if they die or are destroyed by any injury.

The brain is usually divided into the brain stem and the forebrain, and it is the latter that contains the cerebral hemispheres. Figure 1.1 shows the way in which most neuroanatomists would regard the structure of the brain. The *brain stem* comprises the hindbrain and the midbrain. The part of the brain stem above the spinal cord is called the medulla oblongata; above this is the pons and the cerebellum. Important functions carried out by the medulla and pons are control of the circulation and respiration. The cerebellum is essential for the control of posture and coordinated movement. The midbrain is mainly composed of nerve fibres connecting the forebrain with the hindbrain and spinal cord.

The *forebrain* is usually divided by convention into diencephalon and telencephalon. The diencephalon contains the hypothalamus, important for the control of the internal environment, and the thalamus which is the penultimate relay station of sensory input to the cerebral cortex. The telencephalon contains the rhinencephalon at one time supposed to be mainly concerned with the sense of smell although now it has become clear that this is only a minor part of its functions. Apart from the olfactory lobe of the rhinencephalon there are the hippocampal and pyriform cortices, whose functions are not known, but are possibly concerned with the processes of memory. The telencephalon also includes the basal ganglia which are masses of nerve cells mainly involved with the control of movement and posture. Last, the telencephalon contains the cerebral cortex, which forms the subject matter of the remainder of this book.

The whole of the forebrain is not essential for life. Congenitally deformed babies without any forebrain (anencephalics) can exist for some time. These anencephalics may have only a spinal cord and hindbrain, the rest of the cranial cavity being filled merely with fluid, yet they are able to breathe, suckle and perform the reflexes associated with activity in the

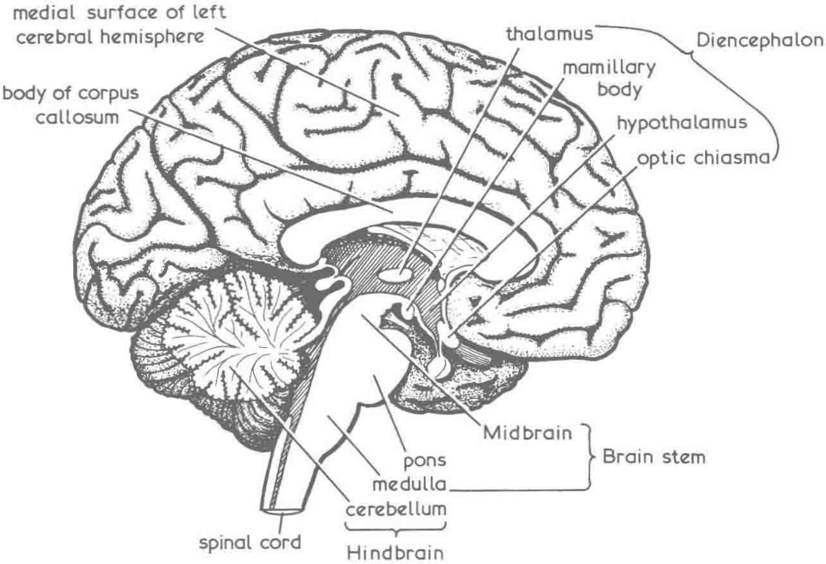


Figure 1.1 Medial sagittal section of human brain. This view of the left side of the brain shows the location of the brain stem (hindbrain plus midbrain) and parts of the forebrain (diencephalon plus telencephalon). However, many regions of the telencephalon (e.g. the basal ganglia) cannot be seen in this section of the brain (Modified from Everett, 1971, *Functional Neuranatomy*, 6th Edn. Lea & Febiger, Philadelphia.)

spinal cord. Such a baby sleeps and awakens just like a normal baby, showing that these phenomena cannot be ascribed to activity in the cerebral hemispheres. Other deformed babies lacking a forebrain but with a midbrain, can in addition keep the body temperature at the correct level and adjust the food and water balance. But nevertheless, the cerebrum is necessary for following a normal life in which behaviour is related to environment and in which activity is adjusted to satisfying the needs and drives already mentioned.

The cerebral hemispheres

Most of the forebrain is comprised of the two cerebral hemispheres, the various nuclear masses of grey matter (cells) within them, and the great interconnecting pathways of fibres that join the two across the midline (corpus callosum) and the other pathways that run to and from the spinal cord.

The cerebral hemispheres are interesting from the evolutionary point of view, for they were initially developed in the ancestors of fish to deal with the chemical senses of taste and smell. Even today, smell is the most important sensory modality in the lower mammals, but in primates, keen sight and the visual sense have been developed at the expense of smell. The cerebral cortex reaches the peak of its development in mammals, especially in the primates where it consists of enormous numbers of neurones arranged in the form of a fairly thin sheet. The cells in this sheet of grey matter are arranged in a specialized fashion and it appears that this organization is fundamental to its function, for in those species where the cerebral hemispheres are highly developed and extensive, it becomes greatly convoluted and folded in upon itself, in the form of gyri and sulci, instead of increasing in thickness. However, one should not necessarily equate brain size with intelligence; it is probably the nature and richness of the connections made between the cortical neurones that are of importance. In terms of both absolute size, and size in relation to total body weight, the brain of the dolphin is considerably larger (and more convoluted) than that of the human.

The functions of the cerebral cortex

The cerebral cortex is the grey matter, or the cellular material of the cerebral hemispheres, and forms its outermost layers. The cortex has an input system and an output system, and in this limited sense one might legitimately compare it with any simple ganglion, but of course constructed on a far larger scale. The inputs come, in the main, from the sensory endings in organs such as the eyes, ears, nose, skin, etc. and from other endings actually within the body. The outputs go to muscles and glands and to other parts of the brain. The cortex carries out very many functions which one might consider in terms of its cells being the intermediate neurones interposed between afferent and efferent nerve cells. Cortical neurones, with their rich interconnections, introduce the complex patterns of activity which lead to the continual adaptation of the animal to its environment.

While the spinal cord and much of the remainder of the brain acts in the three dimensions of space, the cerebral cortex adds the dimension of time. Of course events in the spinal cord occur in time as well; what we mean is that an input to the cord initiates neural activity that is complete within seconds or tens of seconds, while neural events initiated in the cortex have consequences that may last a lifetime. The animal's past experience of its environment is stored in the cerebral cortex. This store of learned material influences the carrying out of future adaptive processes which are modified to give the behaviour patterns most appropriate under given circumstances.

The time dimension also enters into the phenomena underlying consciousness, for in the absence of any prolongation in time of sensory experience, it would be impossible to appreciate the ongoing stream of external events. A brief memory trace of sensory input is a necessary feature of consciousness, for it enables the analysis of the mental representation of the external events to be carried out. If one were to be asked in what ways the operation of the cerebral cortex differs from that of a ganglion, the answer would have to include the enormous capacity that the cortex has of storing information over both very short and very long periods of time.

Memory and learning

In his Ferrier Lecture in 1950, J. Z. Young (1951) was forced to admit:

> 'The most obvious failure of current neurophysiological theory is in providing an account of the changing potentialities or plasticity of the nervous system.... The fact that animals learn, that their nervous systems change with use, has been intractable for the physiologist because it has not been easy to find a model that will match the activities of the brain in this respect.'

It is a sad commentary upon the slowness of scientific progress in this field that these sentiments are as true today as the day they were written. We still do not know for certain how information is stored in the brain although, of course, there are many ideas about it. These vary from the view that information storage will eventually prove to be the result of enduring alterations of synaptic efficacy, to the proposal that the growth of nerve fibre terminals and synaptic knobs is the basis of the laying down of new neuronal connections which underlie memory and learning.

In contrast to the bleak picture painted above, we do know quite a lot about the actual properties of memory. We know that it can be disrupted by the passage of fit-producing electric currents (ECT) through the brain, and that it is difficult to lay down memories if protein synthesis is inhibited, but that anaesthetics, whole body cooling, or the loss of consciousness—all of which may abolish ongoing neural electrical activity—do not affect memories. Do these facts give any clue as to the cellular nature of the processes of memory and learning?

At the moment, the explanation for information storage eludes us, probably because any structural changes which are involved at the cellular level take place at the limits of resolution of our investigating techniques. Nevertheless, as we will see in the account of cortical function given in this book, we are slowly amassing information and it may not be too long before we do have an answer to the question.

Structure of the cerebral cortex

Each hemisphere is divided into lobes. In front is the frontal lobe; it is separated by the central sulcus from the parietal lobe and further behind the latter, in the posterior part of the skull, is the occipital lobe. The temporal lobe lies underneath the frontal and parietal lobes, as can be seen in the lateral and ventral views of Figures 1.2 and 1.3.

The body is largely bilaterally symmetrical. We have for example, two legs, two arms, two eyes, and

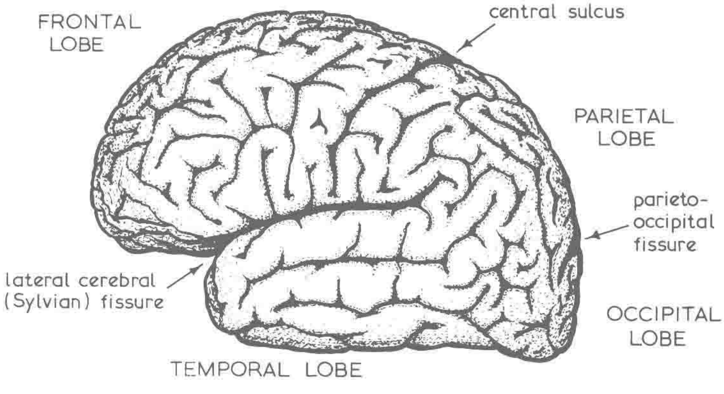


Figure 1.2 Lateral view of the superolateral surface of the left cerebral hemisphere of the human brain. The frontal, parietal, occipital and temporal lobes can be seen. The border between the frontal and parietal lobe is at the central sulcus, and that between the parietal and occipital lobes, at the parietooccipital fissure. The lateral cerebral fissure separates the temporal lobe from the rostral part of the cortex. (Modified from Everett, 1971). *Functional Neuroanatomy*, 6th Edn. Lea & Febiger, Philadelphia.)

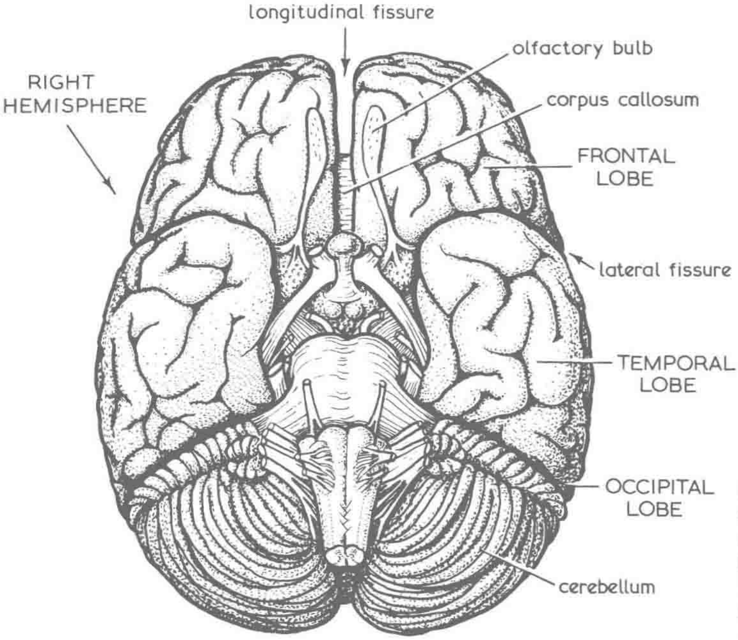
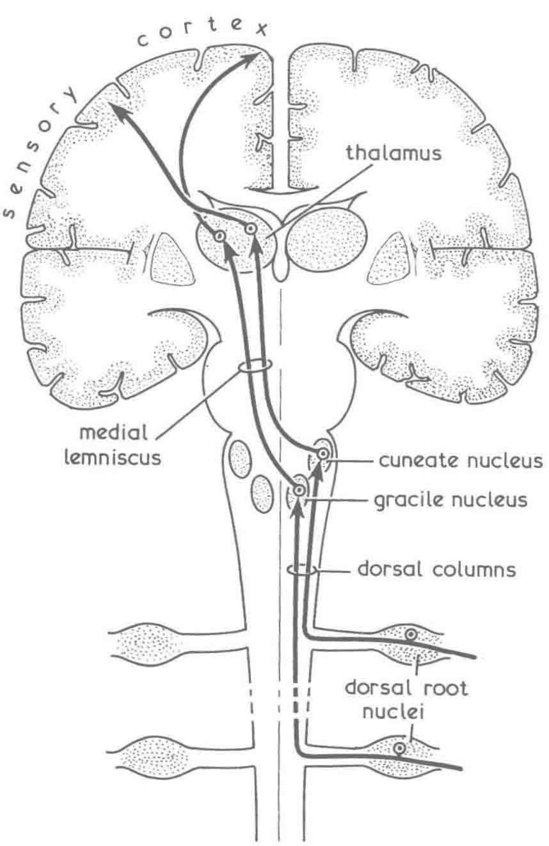


Figure 1.3 shows the ventral surface of both hemispheres of the cerebral cortex, separated by the longitudinal fissure (modified from Everett, 1971, *Functional Neuroanatomy*, 6th Edn. Lea & Febiger, Philadelphia).



two kidneys, etc. This has entailed the evolution of a bilateral brain to deal with the control of the two sides of the body and to receive the inputs from the two eyes. Such a construction plan, of course, might lead to the apocryphal problem of the left hand not knowing what the right hand doeth, so we find that all through the brain the two halves are connected by bridges of nerve fibres called commissures. The most massive of these is the corpus callosum, a great mass of fibre tracts connecting the two cerebral hemispheres across the midline (see Figures 1.1, 1.3).

Plan of working of cerebral cortex

The afferent tracts from the periphery coming into the brain via the spinal cord, go to the thalamus and thence to the cortex. The arrangement of the pathways for somatosensory inputs can be seen in Figure 1.4. The sensory pathways cross the midline and travel to the opposite thalamus and cerebral cortex. In their pathways, the various senses have their own

Figure 1.4 The pathway of some fibres conveying somatosensory information. First order afferents travel in the dorsal roots to the spinal cord where they pass upwards as the dorsal columns to end in synapses within the cuneate nucleus and gracile nucleus. Fibres from these two nuclei cross the midline (as the sensory decussation) and have their terminals on cells in the thalamus, reaching the latter via the medial lemniscus. The thalamocortical radiations transmit impulses from the thalamic nuclei to various regions in the cerebral cortex on the same side.

separate mass of neurones to deal with the incoming information (smell—olfactory bulb; somatosensory input—ventroposterolateral nucleus; vision—lateral geniculate nucleus; sound—medial geniculate nucleus). In Man, each half of the visual field is distributed to one hemisphere. Thus anything which is seen on the left, goes to the right occipital cortex despite the fact that it is seen by both eyes (Figure 1.5). The two occipital lobes are, however, connected by fibres travelling in the corpus callosum. Input from the body is arranged on a similar pattern; in the parietal lobe are the cells which form the terminal stations for the reception of somatic information. This area is connected mainly to the opposite side of the body.

Around these primary receiving areas are adjacent areas of cortex, to which the output from the primary area is distributed widely, each primary neurone being connected eventually to a scattered distribution of neurones. The primary areas are not devoted exclusively to the processing of their own particular sensory modality. They also have inputs from other types of sensation coming from other parts of the body. Thus visual stimuli can affect the somatosensory cells, or auditory stimuli can be detected as impulses in neurones within the motor cortex.

The experience of sensation is associated with electrical activity in the primary receiving areas, although electrical activity in the thalamus is known also to give rise to sensation. If one stimulates the primary receiving areas of the cortex with electrical pulses, peculiar sensations are generated.

The brain substance itself is insensitive to pain and electrical stimulation of most parts of the cortex, unless of very high voltage, goes unnoticed. When somatosensory areas of the cortex are stimulated, unusual, but not painful, sensations result. Patients undergoing brain surgery under local anaesthesia, describe such feelings as 'pins and needles' which they think originate in the corresponding part of the anatomy. When the cortical sensory area for the thumb is stimulated the patient will say he feels something in his thumb. In normal cortex, electrical stimulation never elicits natural sensations. Presumably this is due to the fact that the stimulus activates a mass of neurones quite indiscriminately in a way dependent on their geometry with respect to the current flow and on their relative thresholds of excitability. It is reasonable to suppose that in order for a person to have a 'normal' sensation, the appropriate neurones must be excited and the appropriate pathways between neurones must be utilized. Primary and secondary areas are connected to the association areas of the cortex, areas which, as the evolutionary scale is ascended, become larger and larger. In Man, a very

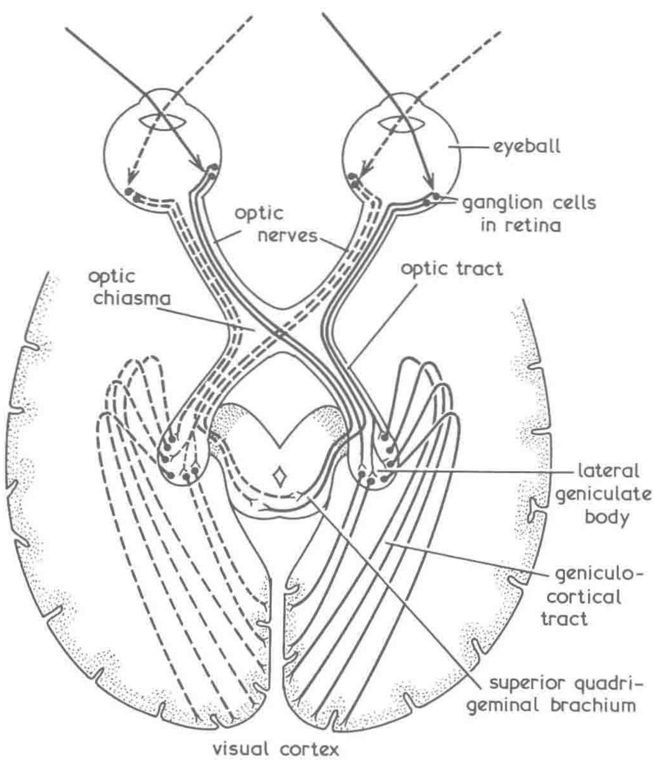


Figure 1.5 Drawing to show the projection of each half of the visual field to the cortex. The left half of the visual field projects onto the nasal half of the left eye and the temporal half of the right eye. Since the axons from the nasal half of the retina cross the midline, the information from the left half of the visual field for each eye is combined in the right hemisphere.