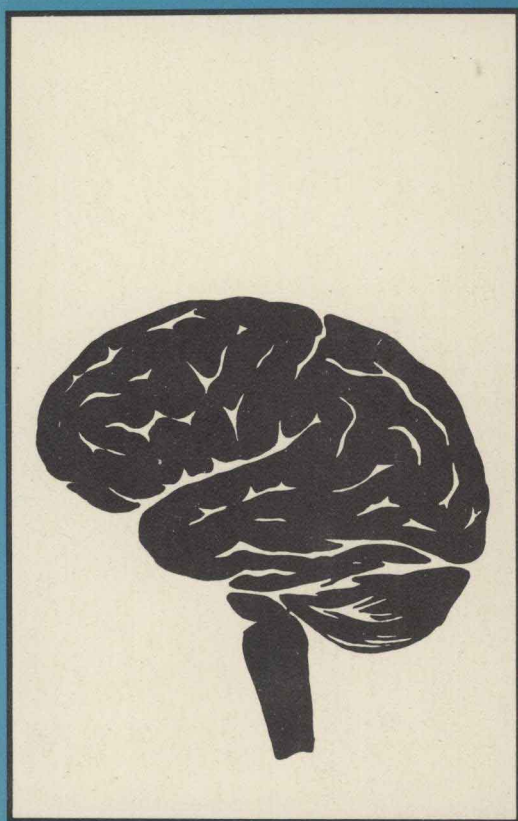


INTRODUCTION TO BIOPSYCHOLOGY



Richard F. Thompson

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HARVARD UNIVERSITY

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PREFACE

Man is an animal, but a very special and unique “psychological” animal. To understand ourselves and our fellow-humans properly we must know something about both our psychology and our biology. This volume serves as an elementary introduction to the biological basis of behavior and experience. Biopsychology goes by many names: physiological psychology, psychobiology, neuropsychology. The basic goal is to understand human behavior and experience in terms of underlying physical and biological mechanisms, particularly the brain and its functions.

This Introduction to *Biospsychology* has been adopted from portions of a more general text (*Psychology*, Harlow, McGaugh, and Thompson, Albion, 1971) and is designed to be used as an elementary text in biopsychology or as supplementary reading for introductory courses in psychology and biology.

Many individuals have contributed to this book. I am indebted to Norman Weinberger for contributing to Chapter 3 (Sleep, Dreaming, and Attention), to Gary Lynch for contributing to Chapter 4 (Motivation), to Gerald McClearn and James McGaugh for their contributions to Chapter 5 (Heredity), and to Nancy Kyle and Cheryl Real for preparing the manuscript, and most particularly to my wife, Judith, for her help and patience.

RICHARD F. THOMPSON

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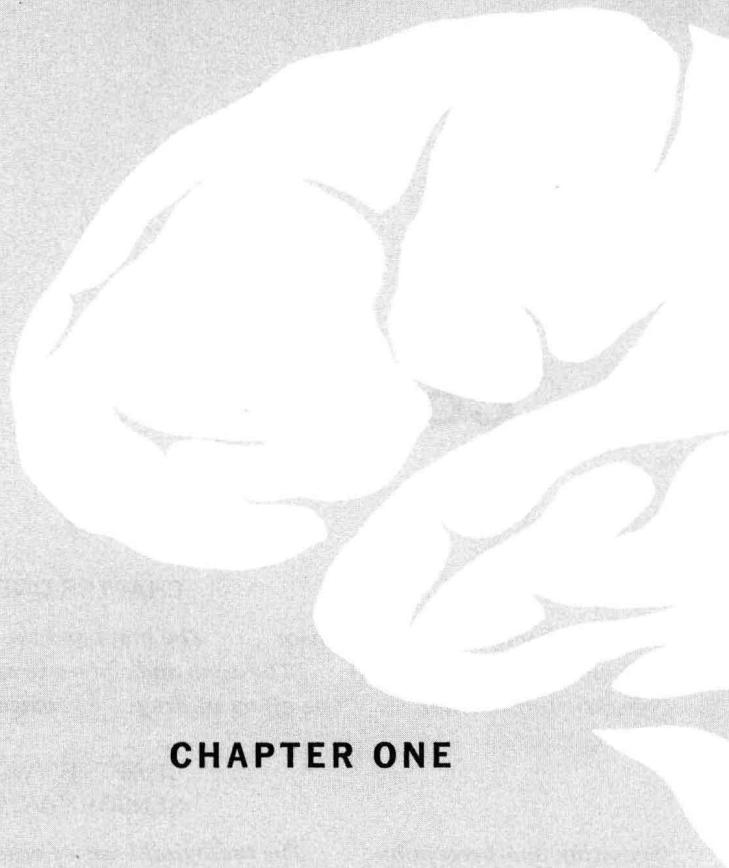
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CHAPTER ONE

THE NEUROLOGICAL BASIS OF BEHAVIOR

Neurobiology is the study of the neural basis of behavior, which comes down to the study of the brain and how it functions to control behavior. The human brain is the most complex structure in the known universe. An average human brain has on the order of 12 billion nerve cells, and the possible number of interconnections and pathways among them in a single brain is greater than the total number of atomic particles making up the universe. The physical basis of everything that we are and do, both as members of the species *Homo sapiens* and as individuals, is to be found in the brain. All our response and behavioral patterns, everything that we have learned and experienced throughout our entire lifetimes, are in some way coded in the brain. Indeed, our actions and subjective experiences are but outward reflections of the patterns of physical activity in the brain. If we could understand the brain we would understand the reasons for all aspects of human behavior.

Although the human brain is an enormously complex mechanism, there are certain principles of organization, in terms of both its structure



NEUROBIOLOGY

and its functions, that permit us to gain a relatively simple overview of what the brain is and how it actually works. The entire field of neurobiology has undergone a major revolution—a knowledge “explosion”—in the past few years, and in the process a great many fundamental and extremely important discoveries have been made about the brain. We shall touch only on some of the highlights of this exciting and many-faceted story.

We are rapidly approaching a level of knowledge and understanding of the brain that will permit us for the first time to determine more about what a person is experiencing by recording the activity from his brain than he is able to describe to us himself, at least in some situations. For example, a wire may be glued to the surface of a person's scalp to pick up the electrical activity, or voltage, that is generated by the underlying brain. Of course these electrical signals are very weak; they are in the microvolt (millionths of a volt) range. The signals are led through an amplifier and are displayed on a polygraph, usually an ink record made on moving paper. This record is termed an *electroencephalogram* (EEG). A simplified version of such a recording device is shown in schematic form in Fig. 1-1.

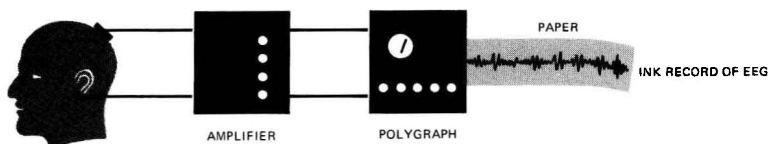


FIGURE 1-1 *General method of recording brain activity in man. Activity is picked up by a wire on the scalp, amplified, and written out on moving paper by a polygraph. The paper record is thus a graph of the changing voltage generated by the brain (on the ordinate) over time (abscissa). The wire on the ear serves as a neutral reference point.*

Examples of EEG tracings are shown in Fig. 1-2. These are simply tracings of the voltages generated by the brain over time. The upper tracing is typical for a person who is alert and attentive; there are few obvious waves, but in general the activity (voltage change) is small, irregular, and fast. The next tracing is typical of a subject who is resting quietly but is awake. A regular rhythmic wave pattern, the *alpha rhythm*, becomes quite clear. The alpha wave occurs at a frequency of about 8 to 12 per second and waxes and wanes. When the subject is asleep and not dreaming the waves tend to be slower than alpha and of large amplitude (this condition is called *slow-wave sleep*). In the last tracing the subject has started to dream. The pattern has become much more like that characteristic of the alert awake state, but the subject is still asleep. If we were to awaken him at this point, he would report that he was dreaming. If we were to wait until he awakened naturally, he would probably be unable to tell us whether he had been dreaming or not, but we could tell with a good degree of accuracy simply by looking at the EEG.

The EEG is a record of the ongoing or spontaneous electrical activity of the brain, measured, of course, at some distance from the brain on the surface of the scalp. It is a kind of overall average of what many thousands or millions of nerve cells in the brain are doing. With the same simple arrangement of a wire glued to the scalp we can also record electrical activity evoked by a stimulus. In the recording setup shown in Fig. 1-1 the recording wire is at the back of the head overlying the visual area of the brain, where visual information is processed. If we suddenly flash a light or a visual pattern in the eye, a relatively clear electrical response will be picked up by the wire on the scalp. The activity is generated by many thousands of neurons in the visual area of the brain. These responses are actually averaged by a computer; individual responses are hard to see because there is so much brain "noise."

A striking example of the information conveyed by the averaged brain response is shown in Fig. 1-3. Simply by noting the characteristics of the responses, we can determine whether the subject is viewing a square or a diamond, regardless of what he chooses to tell us, and regardless of the size of the object. However, if the subject for some reason mistakes the two objects, the brain response seems to correspond to what the subject *thinks* he sees, not what is presented to him. Even more remarkably, if the subject is asked to imagine one of the stimuli,

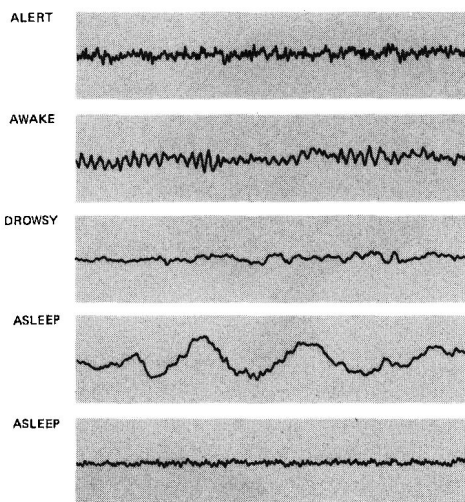
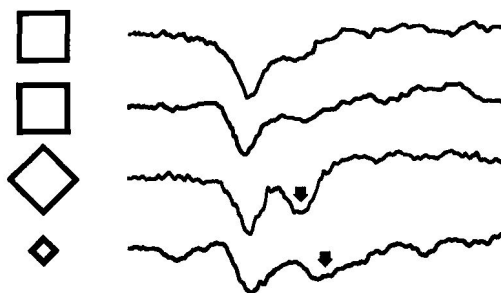


FIGURE 1-2 *Typical human EEGs taken from subjects in different states, ranging from alert wakefulness to deep sleep [Brazier, 1968].*

FIGURE 1-3 *Human averaged evoked potentials. Stimulus forms are shown on the left, and the brain response evoked by each stimulus is shown on the right. Both the square and the diamond evoke the same first wave, but the diamond also evokes a later wave, independent of the size of the diamond. [John et al., 1967]*



the brain response may correspond to the stimulus he is thinking about even when no stimulus is present. This type of averaged brain response may provide us, for the first time, with a way inside the mind—an objective method of measuring mental events.

We shall discuss here only a brief overview of the structural organization of the brain. Each of the regions described will be considered in detail later in connection with the important psychological processes to which they relate, particularly sleep and waking, motivation, sensation and perception. It is perhaps useful at this point to review a few simple definitions. The *brain* refers to the enlarged collection of cells and fibers inside the skull at the head end of an animal; it becomes the *spinal cord* as it leaves the skull (see Fig. 1-4). The *central nervous system* (CNS) includes both the brain and the spinal cord and is composed of nerve-cell bodies and their characteristic fiber processes, glial cells, and a variety of other types of cells making up blood vessels, membranes, etc. A complete nerve cell with its cell body and fibers is called a *neuron*. The functional connection from one neuron

THE BRAIN AND NERVOUS SYSTEM

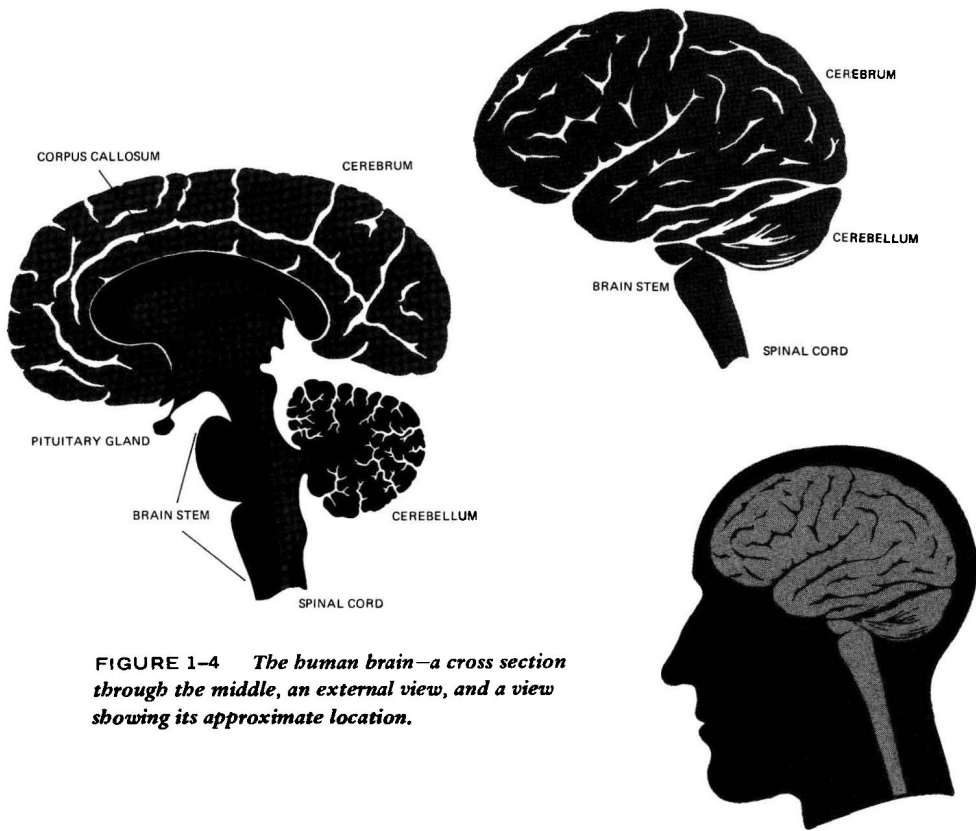


FIGURE 1-4 *The human brain—a cross section through the middle, an external view, and a view showing its approximate location.*

to another is called a *synapse*. The word *nerve* refers to a collection of nerve fibers (not including the cell bodies) outside the CNS; inside the CNS it is called a *tract*. Collections of nerve cell bodies are called *nuclei* if they are inside the CNS and *ganglia* outside.

COMPARATIVE AND DEVELOPMENTAL ASPECTS OF THE BRAIN

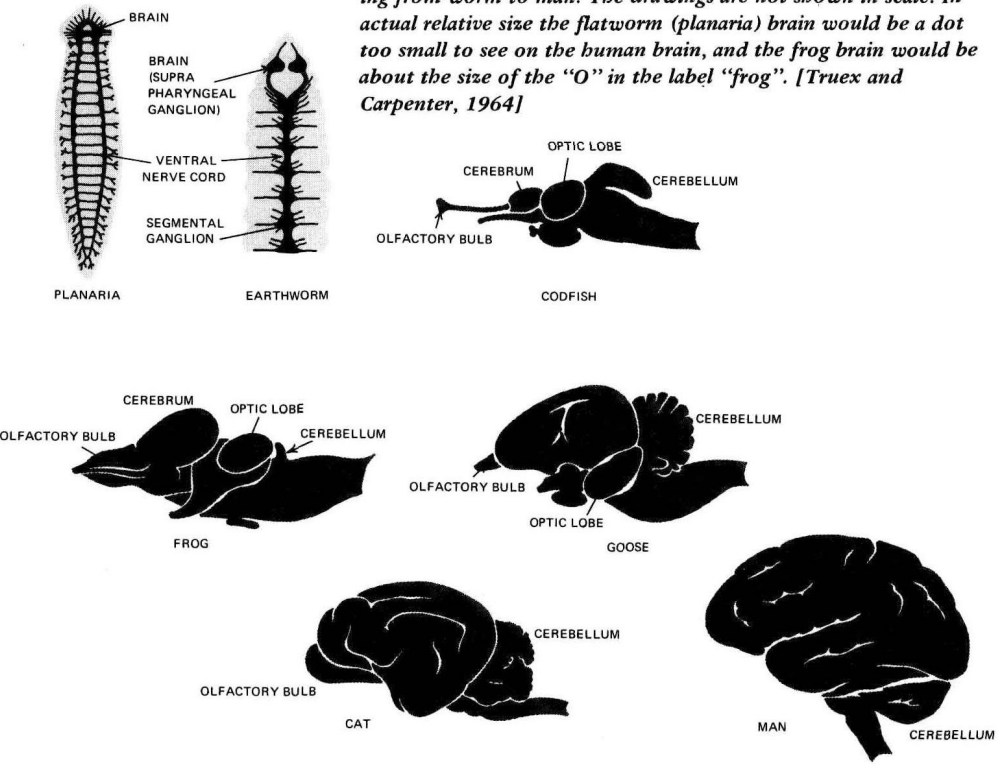
Most of what you see when you look at the brain in Fig. 1-4 is actually a surface structure of the forebrain, the *cerebral cortex*. In man and other higher vertebrates the cerebral cortex has enlarged enormously. In fact it has pushed out over all the rest of the brain, so that the basic tubular arrangement of the nervous system cannot be seen at all in the human brain, even at birth. However, we can get a clearer view of how the brain is formed by comparing the brains of simpler animals with man, and by comparing the adult human brain with the developing brain of the human embryo from early stages after conception to birth.

The basic organization of the vertebrate brain and spinal cord is perhaps most easily seen in certain invertebrates, particularly worms. A series of brains ranging from the flatworm (planaria) and earthworm to

man are shown in simplified form in Fig. 1-5. The fundamental plan is that of a segmented tube. This is evident in the earthworm, where each body segment has nerves going into and out from the corresponding segment of the tubular nervous system. Even in the worm there is an enlargement of the “head” end in relation to specialized receptors. The human brain maintains the basic tubular organization from spinal cord up to about the middle of the brain (midbrain). However, the front end of the tube is enormously expanded and laid back over the core tube to form most of what we usually refer to as the brain.

The hindbrain and midbrain of the human are a continuation of the tubular organization of the spinal cord and resemble the worm nervous system. In mammals the tubular portion of the nervous system is, of course, only relatively tubular. There is a very small central canal filled with *cerebrospinal fluid*. The tube is thus mostly wall, composed of nerve cell bodies and fibers, glial cells, blood vessels, and so on. However, the forebrain of the higher mammals is, as we noted earlier, so enlarged that it becomes most of the brain. It is worth emphasizing that the forebrain differs embryologically from the hindbrain in that they come from different types of primitive tissues. It is this relative enlargement of the forebrain, particularly the cerebral cortex, that distinguishes men from monkeys and monkeys from lower mammals. This is “where the action is” in the control of complex behavior.

FIGURE 1-5 The general appearance of a series of brains ranging from worm to man. The drawings are not shown in scale. In actual relative size the flatworm (*planaria*) brain would be a dot too small to see on the human brain, and the frog brain would be about the size of the “O” in the label “frog”. [Truex and Carpenter, 1964]



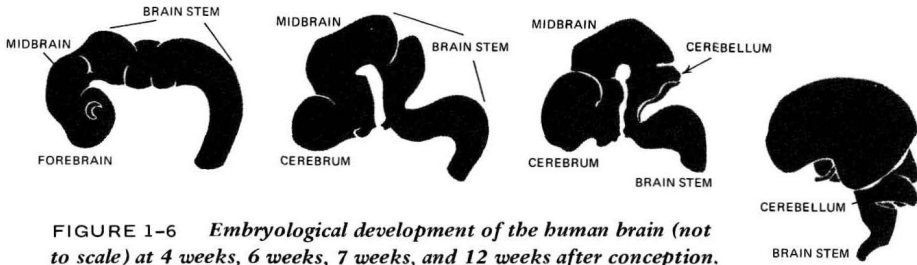


FIGURE 1-6 *Embryological development of the human brain (not to scale) at 4 weeks, 6 weeks, 7 weeks, and 12 weeks after conception. The brain at 12 weeks is actually 10 times larger than it is at 4 weeks. [Peele, 1954]*

It is a fundamental biological principle that “ontogeny recapitulates phylogeny”—that is, in embryological development the individual organism passes through many of the forms that comprise its evolutionary history. As the novelist Aldous Huxley [1928] put it:

... something that has been a single cell, a cluster of cells, a little sac of tissue, a kind of worm, a potential fish with gills ... [will] one day become a man.

This principle is clearly illustrated by the developing human nervous system. Some of the embryological stages of the human brain are shown in Fig. 1-6. The brain of the 5-millimeter embryo is basically similar to the primitive vertebrate adult brain. However, there is already a sharp bend in the midbrain. By the time the embryo is 11 millimeters long the brain shows several subdivisions and is beginning to fold back on itself. At 15 millimeters the cerebrum is beginning to grow out, as is the cerebellum. Finally, the brain of the 53-millimeter embryo shows a marked similarity to the adult brain, although the cerebrum has not yet grown out to cover the midbrain.

ANATOMY OF THE NERVOUS SYSTEM

THE PERIPHERAL NERVOUS SYSTEM The *peripheral nerves* are the nerves lying outside the central nervous system which connect to skin, muscles, and glands. There are in fact *two* peripheral nervous systems, the somatic system and the autonomic system. Each contains both sensory and motor nerves, but their functions are quite different. The *somatic nervous system* controls all the striated muscles—the muscles that we contract when we walk, write, talk, make all types of voluntary motions, and make involuntary adjustments in posture and other reflex functions. The somatic motor nerves thus control most of what we normally call behavior. The *autonomic nervous system*, in contrast, controls glands, smooth muscles and the heart, and what might be called the emotional aspects of behavior. Crying, laughing, fear, anger, and love involve the autonomic nervous system. Sensory input to the somatic nervous system is from skin, joint, and muscle receptors and includes touch, pressure, temperature, and pain. Sensory input to the auto-

onomic nervous system is from glands and smooth muscle and is generally much more diffuse, conveying a vague sense of feeling, pain, and organic sensations.

To add to the confusion there are two subdivisions of the autonomic nervous system, the *sympathetic* and *parasympathetic*, which have their ganglia in different locations. Often the functions of the two systems are opposite. Activation of the sympathetic system causes contraction of arteries, acceleration of the heart, inhibition of stomach contractions and secretion, and dilation of pupils, whereas activation of the parasympathetic system causes dilation of arteries, inhibition of the heart, stomach contractions and secretions, and constriction of pupils. It appears that the sympathetic system functions to mobilize the resources of the body for emergencies, whereas the parasympathetic system tends to conserve and store bodily resources. Thus in a sudden emergency a person will experience increased heart beat, inhibition of stomach activity, widening of pupils, and energy mobilization as a result of the sympathetic system. Such conservative functions as digestion, basal heart rate, and bladder control are carried on in periods between stresses by means of the parasympathetic system.

THE SPINAL CORD Two general categories of activity are handled by the spinal cord. *Spinal reflexes* are muscular and autonomic responses to bodily stimuli which occur even after the spinal cord is severed from the brain, as in a paraplegic accident victim. In addition, a wide variety of *supraspinal* activity is channeled through the spinal cord. The cerebral cortex and other brain structures controlling movement of the body convey activity down the spinal cord to motoneurons, which in turn control the muscles, and all bodily sensations are conveyed up the spinal cord to the brain. Analogous sensory and motor relations for the head are handled directly by the cranial nerves, which are like peripheral nerves but go directly to the brain rather than to the spinal cord.

THE BRAIN STEM The *brain stem* refers to the structures of the mid-brain and hindbrain, which are overlain by the cerebral hemispheres as indicated in Fig. 1-4. The hindbrain represents the continuation and expansion of the spinal cord in the brain and contains all the ascending and descending fiber tracts interconnecting brain and spinal cord, together with a number of important nerve-cell nuclei. The vital autonomic control nuclei concerned with respiration, heart action, and gastrointestinal function are located in the lower brain stem.

The brain stem *reticular formation* has extremely important functions which have only recently been appreciated. Anatomically it is a complex mixture of cell bodies, fibers, and nuclei extending from the spinal cord to the cerebrum, generally located in a somewhat ventral (lower) position in the brain stem (see Fig. 1-7). The two major aspects of reticular function concern descending influences on spinal and cranial motoneurons and ascending influences on the cerebral cortex and other brain structures. Stimulation of descending portions of the reticular system

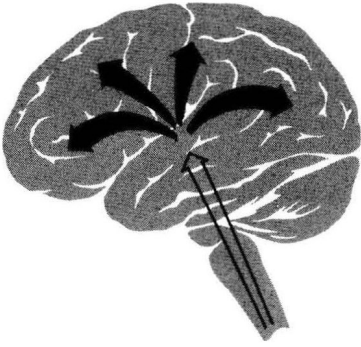


FIGURE 1-7 *The ascending reticular system, shown as a large central arrow that acts upward and outward on the brain [Magoun, 1954].*

may cause either decreases (inhibition) or increases (facilitation) in the activity of the motoneurons controlling the skeletal musculature. In a classic paper Moruzzi and Magoun [1949] demonstrated that stimulation of the ascending reticular formation, or the ascending reticular activating system, resulted in an arousal response on the EEG, a pattern of low-voltage fast cortical activity characteristic of the waking state (see Fig. 1-2). Destruction of the midbrain reticular formation tends to yield a sleeping or stuporous animal [Lindsley et al., 1949].

The ascending reticular formation thus appears to be critically involved in the control of sleeping and waking. It also seems to play a fundamental role in behavioral alerting and possibly in attention as well [Lindsley, 1958]. The reticular formation receives input from all sensory systems and is in fact the major ascending system for the pathways mediating pain. Still another very old brain stem system that has acquired a new significance is the *raphé nuclei*. These are groups of cells lying in the midline and extending throughout the brain stem. There are relatively few neurons in the raphé system, but they seem to play a significant role in regulation of sleeping and waking and form a very important chemical circuit in the brain.

The brain stem developed early in the course of evolution and is surprisingly uniform in structure and organization from fish to man. There are, of course, some variations among species. A general principle of neural organization is that the size and complexity of a structure is related to the behavioral importance of that structure. In fish, which have no cerebral cortices, the midbrain region contains the important centers of seeing and hearing and is relatively large. Among mammals, the bat, for example, has a much enlarged midbrain auditory nucleus, corresponding to its extensive use of auditory information. As you probably know, the bat employs a system much like sonar. It emits very-high-frequency sound pulses and determines the location of objects in space by the echo sounds of the reflected pulses. The relationship of size of structure to behavioral importance provides a number of clues about possible functions of the various brain structures.

In summary, the brain stem contains all the fiber systems interconnecting the higher brain structures and the spinal cord; it also con-

tains the cranial nerves and their nuclei (except for the olfactory and optic nerves), nuclei subserving vital functions, emotional expression, and many higher-order nuclei concerned with various sensory modalities. When all brain tissue above the midbrain is removed in a cat, for example, the animal is still capable of an amazing variety of behaviors. It will live for long periods, can walk, vocalize, eat, sleep, exhibit some components of emotional expression, and may even be capable of very limited learning [Bard and Macht, 1958]. Humans, on the other hand, rarely survive if all tissue above the midbrain is absent or destroyed, and if they do, they exhibit only primitive reflex responses.

THE CEREBELLUM AND BASAL GANGLIA The cerebellum is in evolutionary terms a very old structure and was probably the first to be specialized for sensory-motor coordination. It overlies the brain stem (see Fig. 1-4) and is typically very much convoluted in appearance, with a large number of lobules separated by fissures. The cerebellum is basically similar from snake and fish to man. Although it may be involved in a number of other functions as well, the cerebellum is primarily concerned with the regulation of motor coordination. Damage to the cerebellum produces characteristically jerky, uncoordinated movement.

The *basal ganglia* are a group of large nuclei (ganglia is really a misnomer) lying in the central regions of the cerebral hemispheres. These nuclei appear to play an important but as yet poorly understood role in the control of movement. Although their specific functions remain a mystery, we are beginning to learn something about a most interesting and important chemical circuit involving the basal ganglia.

THE HYPOTHALAMUS AND LIMBIC SYSTEM The hypothalamus encompasses a group of small nuclei that lie generally at the base of the cerebrum close to the pituitary gland, or *hypophysis*. The pituitary gland, the "master gland" of the endocrine glands, is actually controlled by neurons from the hypothalamus. In recent years it has been found that the interrelationships between these two structures are critical in the neural regulation of endocrine gland function. The very small nuclei that comprise the hypothalamus are of fundamental importance to the entire organism. They are critically involved in eating, sexual behavior, drinking, sleeping, temperature regulation, and emotional behavior in general. The hypothalamus is the major central brain structure concerned with the functions of the autonomic nervous system, particularly with its sympathetic division.

The hypothalamus interconnects with many regions of the brain. A number of these structures, including old regions of the cerebral cortex (the cingulate gyrus), the hippocampus, the septal area, the amygdala, portions of the reticular formation, and the hypothalamus itself, are viewed by many anatomists as an integrated network of structures called the *limbic system* (see Fig. 1-8). Many of these structures seem to be involved in aspects of behavior such as emotion, motivation, and reinforcement.

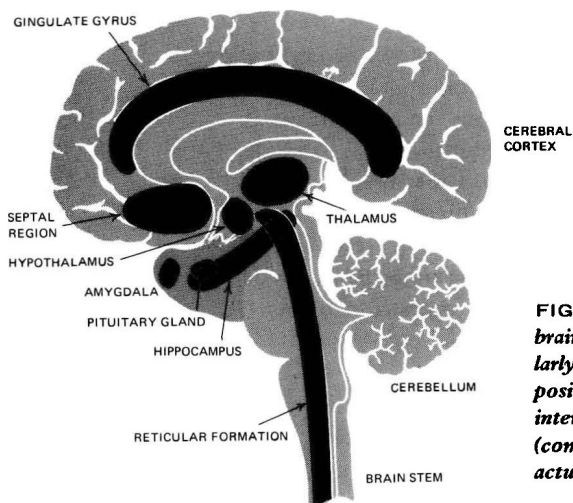


FIGURE 1-8 *The limbic system of the human brain. These older structures are involved particularly in activation, motivation, and emotion. The position of the thalamus, a newer structure with interrelations to the limbic system, is also shown (compare with Fig. 1-4). The limbic structures are actually within the hemisphere, not on the midline.*

THE THALAMUS The thalamus is a large grouping of nuclei located just above the midbrain. Its general shape is somewhat like that of small footballs, one in each cerebral hemisphere (see Fig. 1-8). One region of the thalamus, the lateral or sensory thalamus, is concerned with relaying sensory information to the cerebral cortex from specific sensory pathways for vision, hearing, touch, taste, and perhaps pain. Another region of the thalamus, the diffuse thalamic system, does not seem to be involved in relaying specific sensory information, but it plays an important role in the control of such processes as sleep and wakefulness and is considered a part of the limbic system.

THE CEREBRAL CORTEX Biopsychologists have long been particularly fascinated by the structure and functions of the cerebral cortex. A number of considerations justify viewing this structure as the major system for the more complex and modifiable aspects of behavior. The cerebral cortex represents the most recent evolutionary development of the vertebrate nervous system. Fish and amphibians have no cerebral cortices, and reptiles and birds have only a rudimentary indication of one. More primitive mammals such as the rat have a relatively small, smooth cortex. As the phylogenetic scale is ascended, the amount of cortex relative to the total amount of brain tissue increases accordingly. In more advanced primates such as the rhesus monkey, the chimpanzee, and man the amount of cerebral cortex is enormous and disproportionately large. Of the approximately 12 billion neurons in the human brain, 9 billion are found in the cerebral cortex. There is a general correlation between the cortical development in a species, its phylogenetic position, and the degree of complexity and modifiability characteristic of its behavior.

All incoming sensory systems project to the cortex, each to a specific region. Motor systems controlling the activity of muscles and glands arise in other regions of the cortex. Interestingly enough, the basic organization of the cortical sensory and motor areas does not appear to differ markedly from rat to man. However, with ascending position

on the evolutionary scale there is a striking increase in the relative amount of *association* cortex—areas that are neither sensory nor motor and have often been assumed to be involved in higher or more complex behavioral functions. Studies done on monkeys indicate that the different association areas of the cortex may play rather different roles in the mediation of complex intellectual processes. In particular, the frontal areas (frontal lobes) may be concerned more with short-term memory and the temporal areas with processing of complex sensory information [Harlow, 1952] . Rough-scale drawings of the cerebral cortex in rat, cat, monkey, and man are shown in Fig. 1-9. Note the remarkable increase in absolute brain size, the increase in the number of indentations or fissures, and the increase in relative amount of association cortex. The depths of the fissures are also covered by cerebral cortex. In fact the development of fissures permits a vast expansion of the amount and total area of the cerebral cortex; the human brain has more cortex in the fissures than on the outer surface.

Man, incidentally, does not have the largest brain. The porpoise, the whale, and the elephant all have larger brain masses, although the packing density of cells may be less. The cortex is a multiple layer of nerve cells about 2-millimeters thick which overlies the cerebrum. An actual photomicrograph of a cross section of the visual area of the cerebral cortex in a human brain is shown in Fig. 1-10.

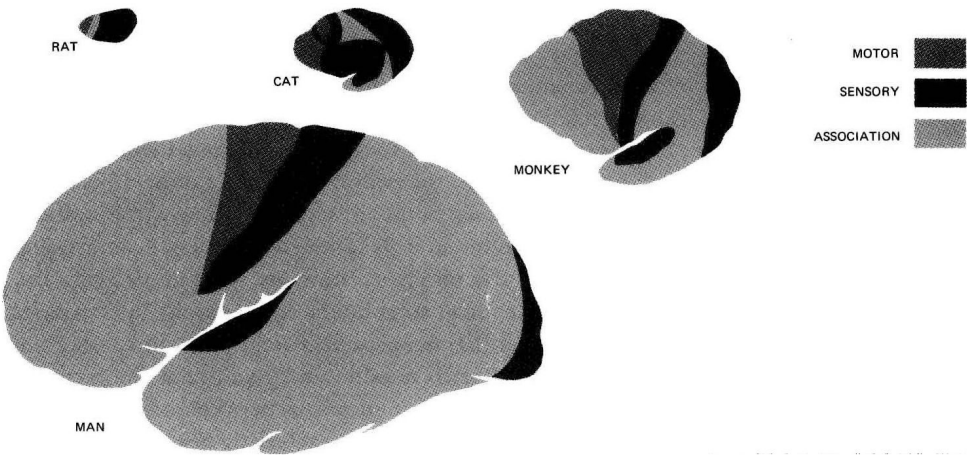


FIGURE 1-9 *Rough scale drawings of the cerebral hemispheres of four mammals. Note the increase both in size and in the relative amount of association cortex. [Thompson, 1967]*

FIGURE 1-10 *Photomicrograph of a cross section through the visual area of the human cerebral cortex. The surface of the cortex is at the top. Each small dot is a neuron. [Sholl, 1956]*