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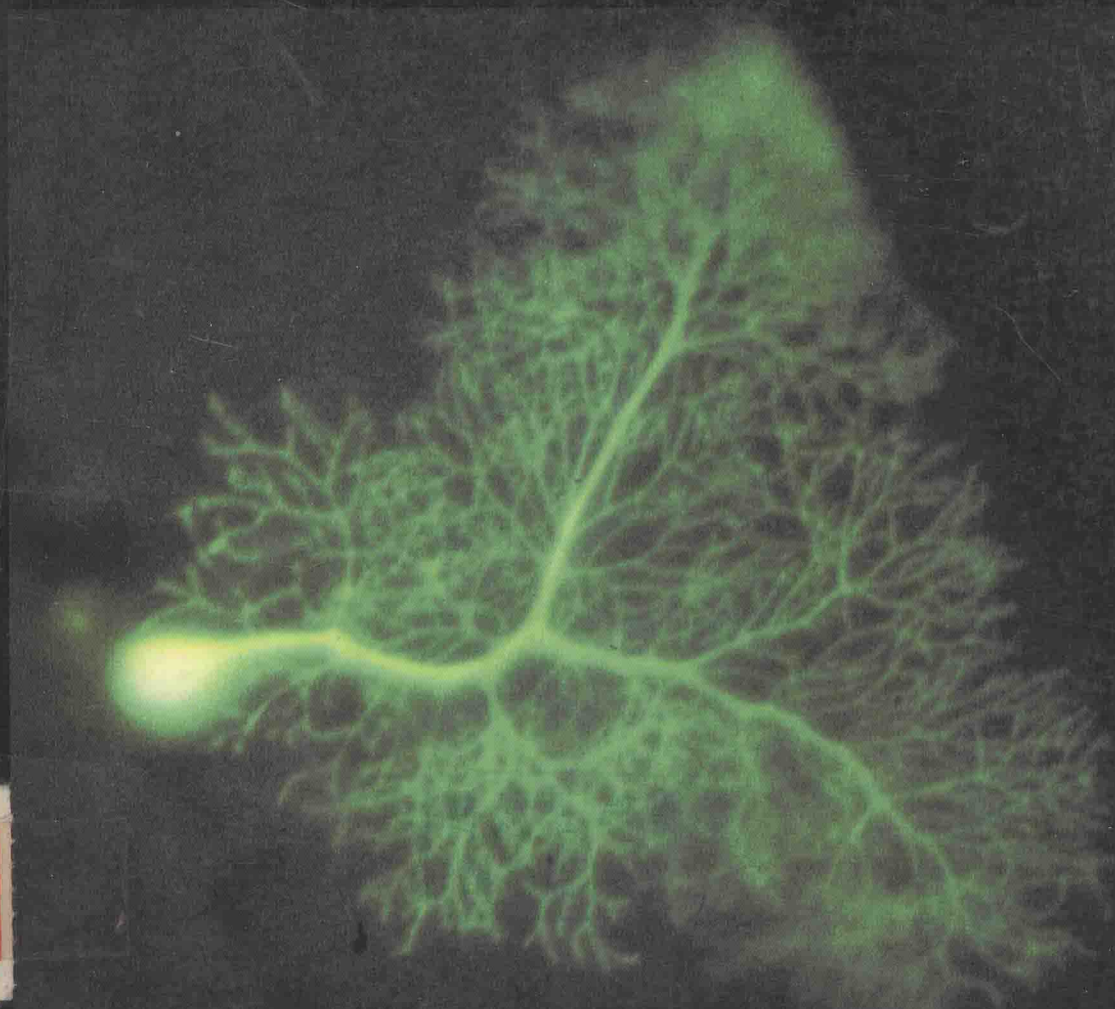
The Biology of the Brain

From Neurons to Networks

RODOLFO R. LLINÁS



The Biology of the Brain

From Neurons to Networks

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SCIENTIFIC AMERICAN
MAGAZINE

Edited by

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W. H. FREEMAN AND COMPANY
New York

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Library of Congress Cataloging-in-Publication Data

The Biology of the brain.

Collection of articles previously published in Scientific American, 1977–1988.
Bibliography: p.
Includes index.
1. Brain. 2. Neurophysiology. I. Llinás, Rodolfo R. (Rodolfo Riascos), 1934– II. Scientific American.
[DNLM: 1. Brain—physiology—collected works. 2. Neurobiology—collected works. WL 300 B6156]
QP376.B623 1989 612'.82 88-36263
ISBN 0-7167-2037-X

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Printed in the United States of America

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The Biology of the Brain

Introduction

Neuroscience has experienced an explosive development over the past fifteen years. An unprecedented increase of knowledge and the variety and power of the new techniques of study have served as the impetus for assembling this book. Among the significant events of this period in neuroscience has been the realization that understanding the workings of the brain requires a multidisciplinary approach. Thus, neuroscience has been released from the constraints of particular sets of techniques and disciplines and has become one of the most impressive and promising areas of biological and theoretical research. Central to this new approach is the realization of the importance of detailed, quantitative understanding of the basic biophysical and biochemical machinery comprising the molecular constituents of nerve cells. The results gathered during this period represent basic knowledge about the functioning of the nervous system on all levels of evolution.

The central theme of this book reflects the view that, as far as we can tell today, the brain, as complex as it is, can only be understood from a cellular perspective. This perspective has been the cornerstone of neuroscience over the past 100 years. Historically, the question of the relation of the body to the mind was, at best, opaque; the mental attributes of humans were only vaguely related to the attributes of the brain. Despite the increase in our knowledge of brain morphology and function at the end of the nineteenth century and the beginning of the twentieth century, there was still a feeling among many scholars that the nature of human reason might be related to some new and wonderful knowledge totally alien to that which is accessible through the scientific method.

The battle to reduce brain function to that of a "society" of interconnected cellular elements was won with the "neuron doctrine," presented in its clearest form by Ramón y Cajal in 1933. This doctrine proposed that the brain is not an amorphous mass of tissue in which every part is related to every other in a spiderweb fashion, but rather is an exquisitely organized society of totally separate nerve cells. Moreover, this doctrine, which is universally accepted today, states that every individual neuron has a particular function and form and, most importantly, a particular set of connections to other neurons. Accordingly, only when the brain was seen to be a cellular society where each element integrates information individually did the complexity of the brain machinery begin to emerge.

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Today, while many neuroscientists suspect that understanding the mind means understanding the properties of sensory motor transformations that ultimately rule brain function, others adhere to the dualist view that mind and brain are separate entities. Regardless of one's view, the fact remains that the scientific method is our only tool in the struggle for knowledge and understanding. Thus, the chapters in *The Biology of the Brain* tell the story of some attempts by scientists to comprehend the nature of the brain and its function by studying the properties of individual cellular elements.

The Neuron

If the brain is a cellular ensemble, its function must be inscribed in the properties of neurons and their synaptic connectivity—that is, in the spontaneous electrical activity of individual neurons derived directly from their intrinsic membrane properties and their connectivity with other neurons. According to this view, the functional properties of the brain arise not merely from the information transmitted by pathways from cell to cell, but also from the specific intrinsic properties of each of the neuronal elements in the transmission chain.

Chapter 1, "The Neuron," by Charles F. Stevens, reviews the functional aspects of individual neurons. Stevens discusses in some detail the properties of the protein molecules that traverse the external surface membrane of the cell and how this protein links the inside of the cell with its extracellular environment. Among other functions, these large protein molecules allow ions to move across the membrane and thus generate ionic currents. The role of the various membrane-specific components in cell communication through the genesis of the so-called action potential (the nerve impulse) and synaptic-transmitter release is also discussed as molecular biology is brought into the context of neuron physiology.

Communication between Neurons

Communication between brain cells is fundamental to the mechanism by which neurons generate brain function. This communication occurs mainly, but not uniquely, through the release of chemical substances. Chemical communication among nerve cells takes many forms; it may be fast and specific, as it is in synaptic transmission, or it may occur slower and less specifically, as with hormones. In the first instance, specificity means the existence of a direct contact between given nerve cells. In the case of a hormone, the message is specific only to groups of cells that have receptors for the hormone being released. Although the modes of communication by neurotransmitter and hormones are quite different, it has been found recently that the messenger molecules used in these two modes have much in common. In fact, the same molecule may appear in both types of communication. This is the subject of Chapter 2, "The Molecular Basis of Communication between Cells," by Solomon H. Snyder. While hormones and neurotransmitters have different physiological effects, these messenger molecules are, in other respects, quite similar. This is made clear by Snyder's discussion of the production, release and regulation of sex hormones (estrogens and progesterone). Peptide hormones are also reviewed since some of them (for example, cholesystokinin) also act as neurotransmitters.

This brings us to one of the most exciting discoveries in neuroscience, the class of molecules known as neuropeptides. The enkephalins were chosen by Snyder to exemplify the properties of these molecules. The discovery of neuropeptides demolished two widely held views: one, that transmitters convey only simple "on" (excitation) of "off" (inhibition) messages, and two, that a given presynpatic cell will release a single type of neurotransmitter. (Neuropeptides are also discussed in detail in Chapter 8.)

Neurotransmitters may also bind to second messengers, triggering a cascade of intracellular reactions that have a slow as well as an immediate effect on postsynaptic cells. Second messengers are molecules that trigger biochemical communication between different parts of a cell. The existence of second messengers and the question of how they regulate the biochemistry, cell biology and even the genomic expression of a neuron adds a new and exciting dimension to the study of neuronal function. This topic is covered in Chapter 3, " 'Second Messengers' in the Brain," by James A. Nathanson and Paul Greengard. It demonstrates that nerve cells may be as complex as the circuits in which they are imbedded. The duration of second messenger-mediated events has led the authors to suggest that such events may provide a basis for long-term changes in the nervous system.

As opposed to the slow action of hormones, fast, discrete and specific communication is generally subserved by presynaptic elements releasing neurotransmitter substances that bind to specific receptor molecules on the postsynaptic membrane. In Chap-

ter 4, "Calcium in Synaptic Transmission," I detail the manner in which transmitter is released following the entry of calcium into the presynaptic terminal of the stellate ganglion in the giant squid. A central issue in that chapter is that synaptic transmission is a variation on the theme of secretion and, indirectly, on that of growth. In order for a cell to release transmitter it must fuse internal reservoirs of transmitter substance (membranous microbubbles) with its outer membrane so that the transmitter substance can be secreted. This process is called exocytosis and it is the mechanism by which transmitter and hormones are released to the fluid outside the cell. It is also a mechanism for adding new membrane to the outer cell surface and thus is a form of cell growth.

Among the most important properties of the nervous system is its ability to retain solutions to sensory or motor events that have proven useful in past circumstances. This issue is addressed under the general rubric of memory and learning. Although it is true that these terms entail a complex set of functions probably subserved by many biological mechanisms at many different levels of organization, it is nevertheless essential that we understand the relation of memory and learning to single-cell physiology. The work of Eric Kandel and his colleagues (Chapter 5, "Small Systems of Neurons") illustrates that possible cellular and molecular mechanisms may implement memory in the invertebrate aplysia. This work has led to our understanding of an exciting chapter in neuroscience.

Neurotransmitters

Chapters 6, 7 and 8 concern three quite different aspects of neurotransmitters. Chapter 6, "The Chemical Differentiation of Nerve Cells," by Paul H. Patterson, David D. Potter and Edwin J. Furshpan, is largely concerned with the factors that determine chemical differentiation of neurons in tissue culture, in particular those derived from the autonomic nervous system. These neurons normally differentiate into either cholinergic (acetylcholine releasing) or adrenergic (norepinephrine releasing). The authors discovered that this differentiation is dependent on the composition of the extracellular milieu during a critical period of development. Indeed, a large molecule released from non-neuronal cells (for example, from skeletal or heart muscle cells) can influence the expression of transmitter by these neurons. If these substances are added to cultures lacking non-neuronal elements, cholinergic cells appear in proportion to the concentration of these molecules added to the media in which the cells grow.

Electrical activity imposed on young cells may also influence whether these cells will be cholinergic or adrenergic: depolarization prevents the induction of cholinergic properties. This is probably mediated by increased intracellular calcium, this ion entering from the extracellular space upon depolarization. These findings bring up the intriguing possibility that the timing and the type of synaptic inputs from the Central Nervous System (CNS) may influence the chemical differentiation of these neurons.

Chapter 7, "GABAergic Neurons," by David I. Gottlieb, considers one group of neurons in detail, those that release the inhibitory neurotransmitters gamma-aminobutyric acid (GABA), one of the important inhibitory transmitters in the CNS. Two types of receptors have been identified for this transmitter substance: $GABA_A$ (activation increases membrane conductance to chloride) and $GABA_B$ (activation increases membrane conductance to potassium). GABAergic cells are found throughout the CNS, comprising the majority of cells in some regions. Gottlieb describes how the amino acid sequence for the receptor was determined. The exciting news is that many chemically sensitive transmembrane channels may be related and be members of a superfamily of molecules that will provide information on exactly how these channels work and how they evolved, probably from a single common ancestor.

Chapter 8, "Neuropeptides," by Floyd E. Bloom, treats that in detail. Two main types of bioactive peptides are used as examples of peptides with long sequences of amino acids. These structures are well conserved in evolution and appear in many species. One type of peptide has short amino acid sequences in common. This group is exemplified by the endorphins and enkephalins. Cells containing the enkephalins are widely distributed in the brain while the endorphins are localized in the region of the hypothalamus and anterior pituitary gland. Genetic engineering tools have been used to determine the amino acid sequence of these neuropeptides. These cells are found in neuronal networks subserving a wide variety of functions. However, cells secreting structurally similar peptides may not be functionally related.

Peptides are special in other respects. They are synthesized only in the ribosomes (in the soma and dendrites, not the axon or axon terminals) as long peptides that are progressively cleaved by specific enzymes into active forms. Their most significant

difference from other transmitter molecules is their mode of action. As Bloom puts it, they "disenable" other, traditional transmitters, making them less effective. Each peptide interacts with its own receptor, which must be linked with the receptor for the traditional transmitter. The chapter ends with a discussion of how peptides may mediate behavior.

Nerve Nets

Proceeding from the nature of single cells we next take up the mechanisms by which they communicate with one another. Knowledge of the properties of neuron ensembles, or nerve nets, is vital to understanding brain function. Single cells cannot generate brain properties; such properties are produced by the interactions between nerve cells. This interaction gives rise to the brain as an organ in a manner somewhat analogous to that by which human individuals give rise to politics or economics. Understanding nerve nets is thus a key to understanding the relation between the brain and the mind. Perhaps one of the best-known neuronal networks is in the retina, which covers the inner surface of the eyeball and is responsible for the light sensing that initiates the process of visual perception.

The circuit elements of the retina are more complex than originally thought. It is now known that there are distinct subtypes of the five categories of neurons found in the retina; there may be as many as 50 different functional elements in this network. The properties of the amacrine cell that make only dendrite-to-dendrite connections within the retina (they have no axonic process) are particularly fascinating. Although Ramón y Cajal reported many types of amacrine cells as early as 1892, it was not until recently that many of the neurotransmitters in the brain were also found in these cells, allowing its grouping into different classes.

The question is, how do the rules of connectivity between cells in the retina "encode" the light images into messages. In Chapter 9, "The Functional Architecture of the Retina," Richard H. Masland reviews, on the basis of his own elegant work and that from other laboratories, the possible role of four types of amacrine cells in the retina. He shows that in this neuronal society particular classes of nerve cells are given particular functions, that is, cells "specialize" in the same sense as individuals do. The specializations arise from the particular connectivity (who you know in society) and the types of synaptic interactions (what your contacts tell you and what, in turn, you let your next in line know about what you have been told). The first to be considered are the acetlycholine-pleasing cells. These excite ganglion cells (the cells that project to the brain). Amacrine cells specialize in "local" signaling. They do not generate action potentials and thus are capable of activating small regions of a dendrite leading to a graded signal with an exquisite spatial localization.

The second type of amacrine cell in the retina is the AII cell. These cells not only sharpen the response of ganglion cells to light but are important for detection of dim light.

The third type of cell was identified by its transmitter, dopamine. These are few of these cells in the retina and their function is still not clear. The last type of amacrine cell discussed by Masland combines the chemical analogues of serotonin and indolamine. These cells come in five "flavors." Because of their synaptic connectivity they are thought to have a major influence on pathways by which dim light passes through the retina, thus providing five different but parallel pathways for the retina to communicate with the brain.

Transplantation

From a medical and a purely experimental vantage point the question of transplanting nerve cells from one brain (or nerve-cell bank) to another is of immense consequence. However, with few exceptions neuronal replacement continues to be only a promise, although it has had great appeal in the neurosciences. Chapter 10, "Transplantation in the Central Nervous System," by Alan Fine, discusses the manner in which cellular events may be modified by implants. The statement has often been made that the nervous system, once having been built, cannot be rebuilt since central nerve cells do not regenerate. This means that, in principal, the genetic heritage for our brain is simultaneously our great provider and our jailer. It implies that whatever we may do to try to correct brain deficits may be achieved only by modifying that which is already present, and probably only in a very subtle and limited manner. But the possibility, however remote, of modifying neuronal networks in a substantial manner—by implanting new neurons—must be carefully studied because it offers the promise that, even in a limited range, we may for the first time be in the position to help brain-injured patients.

Rodolfo R. Llinás

The Biology of the Brain

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The Neuron

It is the individual nerve cell, the building block. It transmits nerve impulses over a single long fiber (the axon) and receives them over numerous short fibers (the dendrites).

• • •

Charles F. Stevens

September, 1979

Neurons, or nerve cells, are the building blocks of the brain. Although they have the same genes, the same general organization and the same biochemical apparatus as other cells, they also have unique features that make the brain function in a very different way from, say, the liver. The important specializations of the neuron include a distinctive cell shape, an outer membrane capable of generating nerve impulses, and a unique structure, the synapse, for transferring information from one neuron to the next.

The human brain is thought to consist of 10^{11} neurons, about the same number as the stars in our galaxy. No two neurons are identical in form. Nevertheless, their forms generally fall into only a few broad categories, and most neurons share certain structural features that make it possible to distinguish three regions of the cell: the cell body, the dendrites and the axon. The cell body contains the nucleus of the neuron and the biochemical machinery for synthesizing enzymes and other molecules essential to the life of the cell. Usually the cell body is roughly spherical or pyramid-shaped. The dendrites are delicate tubelike extensions that tend to branch repeatedly and form a bushy tree around the cell body. They provide the main physical surface on which the neuron receives incoming signals. The axon extends away from the cell body and provides the pathway over which signals can travel from the cell body for long distances to other parts of the brain and the nervous system. The axon differs from the dendrites both in structure and in the properties of its outer membrane. Most axons are longer and thinner than dendrites and exhibit a different branching pattern: whereas the branches of dendrites tend to cluster near the cell body, the branches of axons tend to arise at the end of the fiber where the axon communicates with other neurons.

The functioning of the brain depends on the flow of information through elaborate circuits consisting of networks of neurons. Information is transferred from one cell to another at specialized points of contact: the synapses. A typical neuron may have anywhere from 1,000 to 10,000 synapses and may receive information from something like 1,000 other neurons. Although synapses are most often made between the axon of one cell and the dendrite of

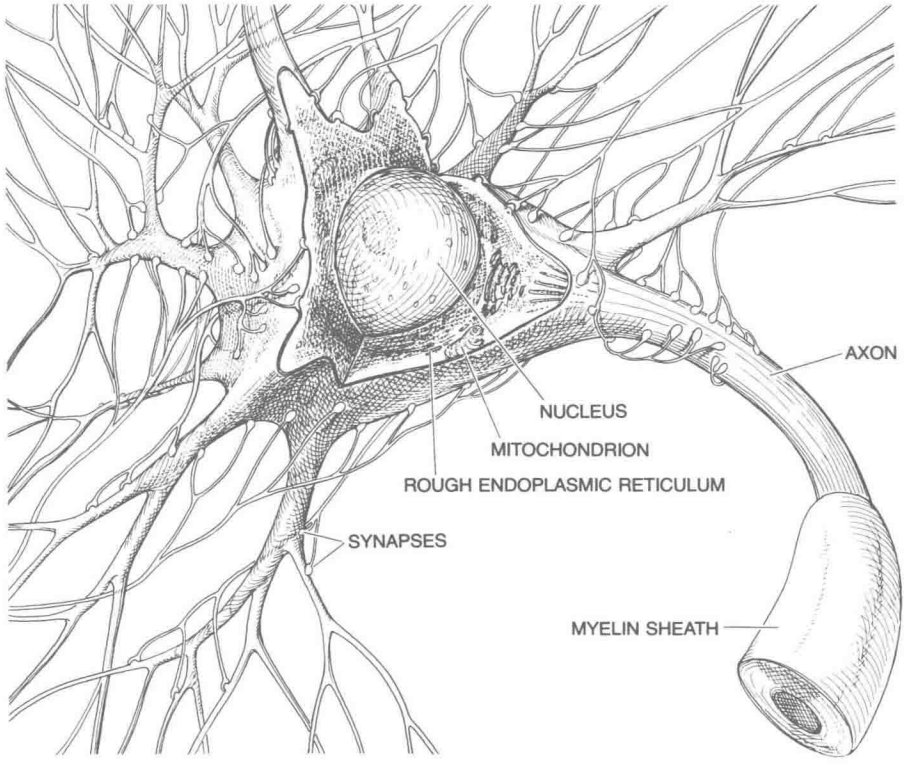


Figure 1 CELL BODY OF A NEURON incorporates the genetic material and complex metabolic apparatus common to all cells, but neurons do not divide after embryonic development; an organism's original supply must serve a lifetime. Projecting from the cell body are several dendrites and a single axon. The cell body and dendrites are covered by synapses. Mitochondria provide the cell with energy. Proteins are synthesized on the endoplasmic reticulum. A transport system moves proteins and other substances from cell body to sites where needed.

another, there are other kinds of synaptic junction: between axon and axon, between dendrite and dendrite and between axon and cell body.

At a synapse the axon usually enlarges to form a terminal button, which is the information-delivering part of the junction. The terminal button contains tiny spherical structures called synaptic vesicles, each of which can hold several thousand molecules of chemical transmitter. On the arrival of a nerve impulse at the terminal button, some of the vesicles discharge their contents into the narrow cleft that separates the button from the membrane of another cell's dendrite, which is designed to receive the chemical message. Hence information is relayed from one neuron to another by means of a transmitter. The "firing" of a neuron—the generation of nerve impulses—reflects the activation of hundreds of synapses by impinging neurons. Some synapses are excitatory in that they tend to promote firing, whereas others are inhibitory and so are capable of canceling signals that otherwise would excite a neuron to fire.

Although neurons are the building blocks of the brain, they are not the only kind of cell in it. For example, oxygen and nutrients are supplied by a dense network of blood vessels. There is also a need for connective tissue, particularly at the surface of the brain. A major class of cells in the central nervous system is the glial cells, or glia. The glia occupy essentially all the space in the nervous system not taken up by the neurons themselves. Although the function of the glia is not fully understood, they provide structural and metabolic support for the delicate meshwork of the neurons.

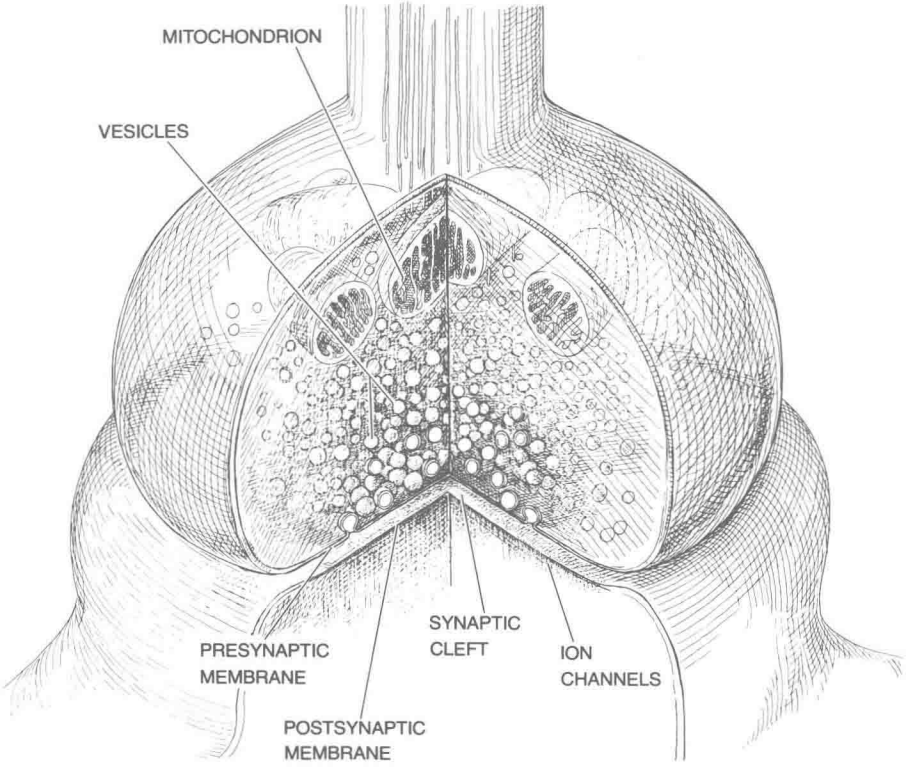


Figure 2 SYNAPSE consists of two parts: the knoblike tip of an axon terminal and the receptor region on the surface of another neuron. The membranes are separated by a synaptic cleft some 20 to 30 nanometers across. Molecules of chemical transmitter, stored in vesicles in the axon terminal, are released into the cleft by arriving nerve impulses and change the electrical state of the receiving neuron, making it either more likely or less likely to fire an impulse.

One other kind of cell, the Schwann cell, is ubiquitous in the nervous system. All axons appear to be jacketed by Schwann cells. In some cases the Schwann cells simply enclose the axon in a thin layer. In many cases, however, the Schwann cell wraps itself around the axon in the course of embryonic development, giving rise to the multiple dense layers of insulation known as myelin. The myelin sheath is interrupted every millimeter or so along the axon by narrow gaps called the nodes of Ranvier. In axons that are sheathed in this way the nerve impulse travels by jumping from node to node, where the extracellular fluid can make direct contact with the cell membrane. The myelin sheath seems to have evolved as a means of conserving the neuron's metabolic energy. In general myelinated nerve fibers conduct nerve impulses faster than unmyelinated fibers.

Neurons can work as they do because their outer membranes have special properties. Along the axon the membrane is specialized to propagate an electrical impulse. At the terminal of the axon the membrane releases transmitters, and on the dendrites it responds to transmitters. In addition the membrane mediates the recognition of other cells in embryonic development, so that each cell finds its proper place in the network of 10^{11} cells. Much recent investigation therefore focuses on the membrane properties responsible for the nerve impulse, for synaptic transmission, for cell-cell recognition and for structural contacts between cells.

The neuron membrane, like the outer membrane of all cells, is about five nanometers thick and consists of two layers of lipid molecules arranged with their hydrophilic ends pointing toward the water on the inside and outside of the cell and with their

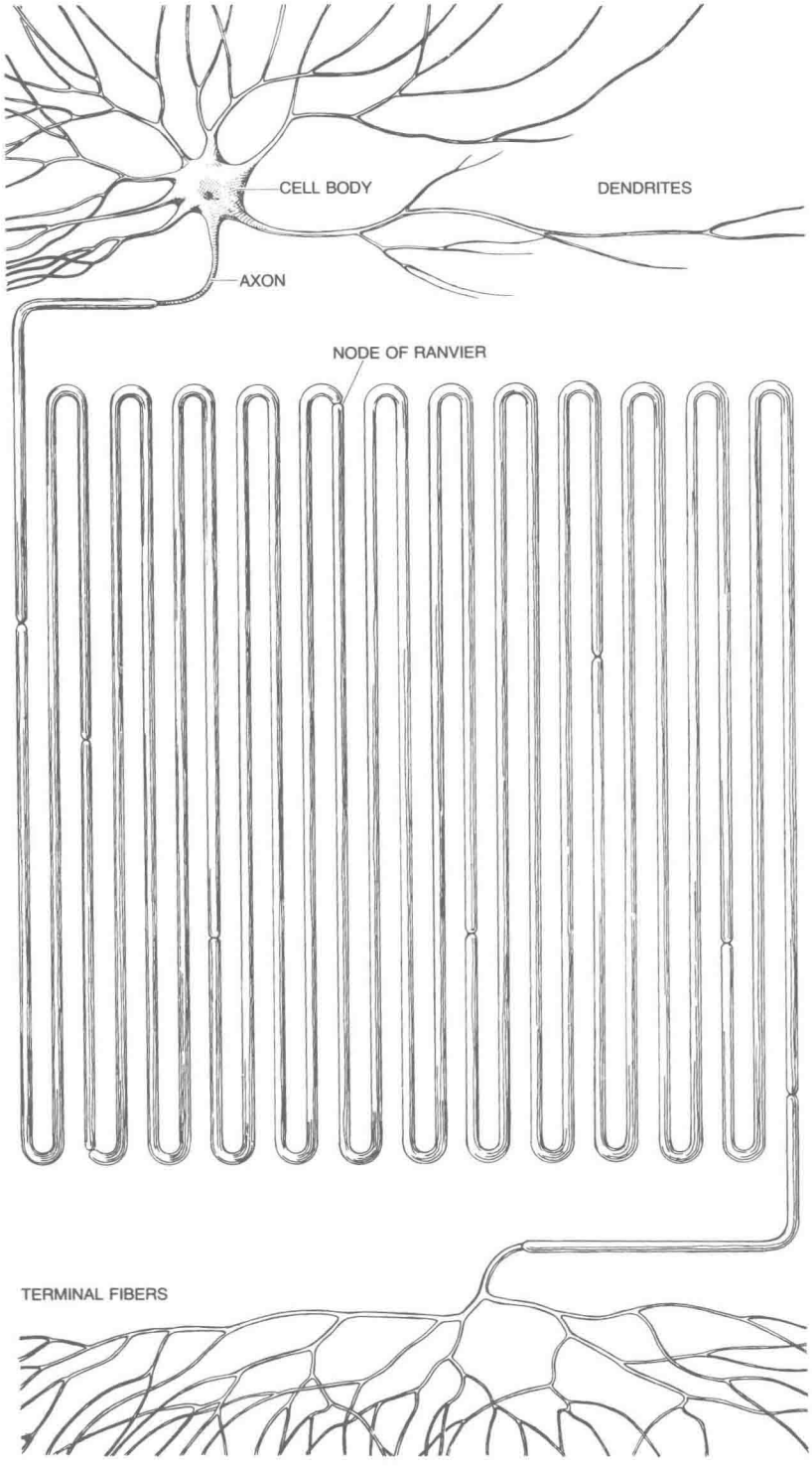


Figure 3 TYPICAL NEURON of a vertebrate animal (enlarged here 225 times) can carry nerve impulses for a considerable distance. The nerve impulses originate in the cell body and are propagated along the axon. This axon, folded for the diagram, would be a centimeter long at actual size, although some axons are more than a meter long. Many axons are insulated by a myelin sheath interrupted at intervals by the regions known as nodes of Ranvier.

hydrophobic ends pointing away from the water to form the interior of the membrane. The lipid parts of the membrane are about the same for all kinds of cells. What makes one cell membrane different from another are various specific proteins that are associated with the membrane in one way or another. Proteins that are actually embedded in the lipid bilayer are termed intrinsic proteins. Other proteins, the peripheral membrane proteins, are attached to the membrane surface but do not form an integral part of its structure. Because the membrane lipid is fluid even the intrinsic proteins are often free to move by diffusion from place to place. In some instances, however, the proteins are firmly fastened down by a substructure.

The membrane proteins of all cells fall into five classes: pumps, channels, receptors, enzymes and structural proteins. Pumps expend metabolic energy to move ions and other molecules against concentration gradients in order to maintain appropriate concentrations of these molecules within the cell. Because charged molecules do not pass through the lipid bilayer itself cells have evolved channel proteins that provide selective pathways through which specific ions can diffuse. Cell membranes must recognize and attach many types of molecules. Receptor proteins fulfill these functions by providing binding sites with great specificity and high affinity. Enzymes are placed in or on the membrane to facilitate chemical reactions at the membrane surface. Finally, structural proteins both interconnect cells to form organs and help to maintain subcellular structure. These five classes of membrane proteins are not necessarily mutually exclusive. For example, a particular protein might simultaneously be a receptor, an enzyme and a pump.

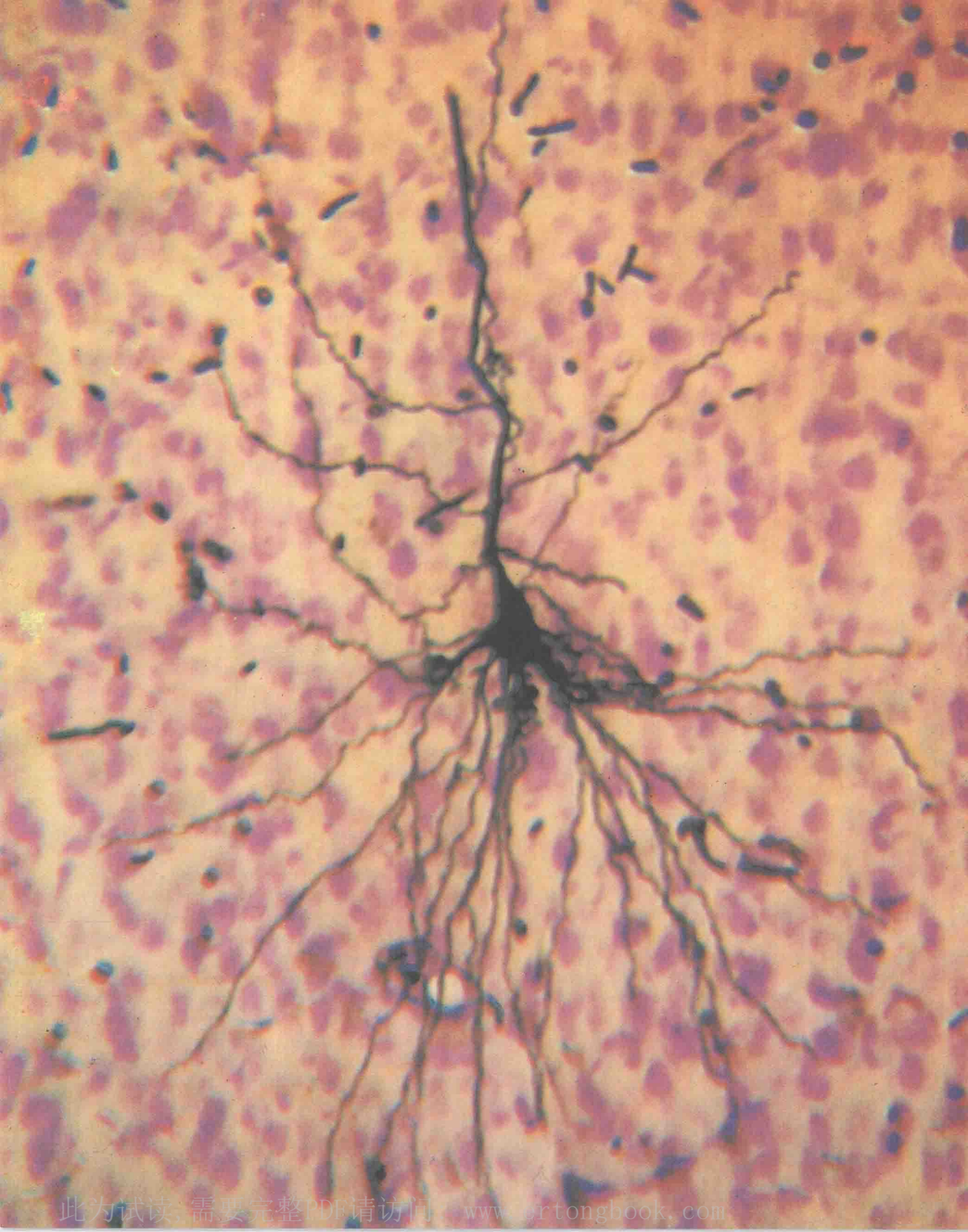
Membrane proteins are the key to understanding neuron function and therefore brain function. Because they play such a central role in modern views of the neuron, I shall organize my discussion around a description of an ion pump, various types of channel and some other proteins that taken together endow neurons with their unique properties. The general idea will be to summarize the important characteristics of the membrane proteins and to explain how these characteristics account for the nerve impulse and other complex features of neuron function.

Like all cells the neuron is able to maintain within itself a fluid whose composition differs markedly from that of the fluid outside it. The difference is particularly striking with regard to the concentration of the ions of sodium and potassium. The external medium is about 10 times richer in sodium than the internal one, and the internal medium is about 10 times richer in potassium than the external one. Both sodium and potassium leak through pores in the cell membrane, so that a pump must operate continuously to exchange sodium ions that have entered the cell for potassium ions outside it. The pumping is accomplished by an intrinsic membrane protein called the sodium-potassium adenosine triphosphatase pump, or more often simply the sodium pump.

The protein molecule (or complex of protein subunits) of the sodium pump has a molecular weight of about 275,000 daltons and measures roughly six by eight nanometers, or slightly more than the thickness of the cell membrane. Each sodium pump can harness the energy stored in the phosphate bond of adenosine triphosphate (ATP) to exchange three sodium ions on the inside of the cell for two potassium ions on the outside. Operating at the maximum rate, each pump can transport across the membrane some 200 sodium ions and 130 potassium ions per second. The actual rate, however, is adjusted to meet the needs of the cell. Most neurons have between 100 and 200 sodium pumps per square micrometer of membrane surface, but in some parts of their surface the density is as much as 10 times higher. A typical small neuron has perhaps a million sodium pumps with a capacity to move about 200 million sodium ions per second. It is the transmembrane gradients of sodium and potassium ions that enable the neuron to propagate nerve impulses.

Membrane proteins that serve as channels are essential for many aspects of neuron function, particularly for the nerve impulse and synaptic transmission. As an introduction to the role played by channels in the electrical activity of the brain, I shall briefly describe the mechanism of the nerve impulse and then return to a more systematic survey of channel properties.

Since the concentration of sodium and potassium ions on one side of the cell membrane differs from that on the other side, the interior of the axon is about 70 millivolts negative with respect to the exterior. In their classic studies of nerve-impulse transmission in the giant axon of the squid a quarter of a century ago, A. L. Hodgkin, A. F. Huxley and Bernhard Katz of Britain demonstrated that the propagation of the nerve impulse coincides with sudden



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