

THE
**CEREBRAL
COMPUTER**

An Introduction to the
Computational Structure
of the Human Brain

ROBERT J. BARON

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Computational Structure
of the Human Brain

ROBERT J. BARON

The University of Iowa



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For all students of brain function

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PREFACE

The human brain is the most complex and powerful computer known. It has been studied intensively for decades and has been the subject of thousands of books, tens of thousands of journal articles, hundreds of university courses, and even several television specials. Among the computational processes that have been investigated are memory, learning, language, visual and auditory perception and recognition, analogical reasoning, thought, attention, planning, and the control of movement. These studies have provided valuable insights into the computational nature of the brain.

However, even with all the advances in our understanding of human information processing, and even with our ever-increasing knowledge of computations in general, including the organization of knowledge, the nature of algorithmic processes and theoretical limits on computability, the human brain continues to elude our understanding. Among the reasons for this elusiveness are its incredible complexity, the redundancy of its circuitry and the variety of different ways that have evolved to reach the same computational goals. Because all of the computational processes which can be brought to bear on a particular problem seem to operate at the same time, the study of any one of them is difficult at best.

Recent investigations, particularly over the past three decades, have markedly increased our understanding of the human brain. Anatomical studies have given us detailed knowledge of the structure of various networks and the connections between them. Combined with clinical investigations, these studies have given major insights into the computations they perform. Clinical investigations, in particular, have characterized abnormalities resulting from localized brain damage. These abnormalities include deteriorated visual, auditory and tactile recognition, impaired language understanding and production, and abnormal planning and control of movement. Each syndrome gives considerable insight into the computational structure of the brain. Particularly with the advent of noninvasive techniques for determining the

focus of damage, researchers are now able to determine the locations of the neural systems which are responsible for the underlying pathology. Neurobiological and neurophysiological investigations have also provided us with information regarding the computations of the various networks of the brain, and as a result, we are beginning to understand not only the biochemical mechanisms that underlie the computations but also details of the computations themselves.

The following excellent books have been written describing the human brain, its structure, its organization, and its function. I will therefore not introduce general topics which are so well presented elsewhere.

Nancy C. Andreasen (1984) *The broken brain*. New York: Harper & Row.

This book has an excellent introduction to the anatomy of the brain, and although its focus is on mental illness, the author describes recent techniques for the study of brain function.

Jack Fincher (1984) *The brain, mystery of matter and mind*. New York: Torstar Books.

This book has exceptionally nice illustrations of the anatomy of the brain but focuses mostly on topics of the mind: language, creativity, intelligence, feelings, and consciousness.

Dick Gilling and Robin Brightwell (1982) *The human brain*. New York: Facts on File.

This book is based on seven BBC-TV programs describing the human brain.

Bryan Kolb and Ian Q. Whishaw (1985) *Fundamentals of human neuropsychology* (2nd ed.). New York: W. H. Freeman and Co.

This excellent book presents both basic background information as well as clear, crisp, and thorough accounts of numerous clinical syndromes.

A. R. Luria (1973) *The working brain. An introduction to neuropsychology*. New York: Basic Books.

This book analyzes various clinical syndromes by showing how they result from damage to the underlying computational systems. Luria emphasizes the computational nature of the human brain.

Richard M. Restak (1984) *The brain*. New York: Bantam Books.

This book is based on the eight-part PBS television series "The Brain."

J. P. Schadé and Donald H. Ford (1965) *Basic neurology. An introduction to the structure and function of the nervous system*. New York: Elsevier.

This textbook presents excellent introductions to four significant areas: neuroanatomy, neurophysiology, neurochemistry, and neuropsychology.

Anthony Smith (1984) *The mind*. New York: Viking Press.

This book presents excellent introductions to the evolution, anatomy, and growth of the brain, in addition to overviews of consciousness, the senses, and ability.

The study of brain function is an interdisciplinary endeavor. My formal training was in mathematics, physics and computer science, but my goal, ever since I began to study the brain in 1966, was to understand how it represents and processes information. This endeavor has forced me to read the literature and talk to researchers in disciplines quite distant from my own. Breaking into an established discipline means learning a new vocabulary and new way of thinking. The process can be overwhelming. One goal, then, in writing this book is to summarize in one place the anatomical, physiological, and clinical facts which are essential for understanding the computational architecture of the brain. I hope to encourage new researchers to study the brain, particularly those individuals with strong mathematical and theoretical talents. Perhaps my effort will keep them from naïvely assuming properties of the brain which simply do not exist. For example, many theorists in the past have studied models of neural assemblies comprised of neurons which are connected together at random. Fortunately, the brain is not built that way, and we have come too far in understanding its structure to condone such naïve assumptions. Chapters in which I have presented fairly standard background material include Chapter 1 (neurons), Chapter 6 (memory), Chapter 7 (the visual system), Chapter 10 (the auditory system), Chapter 12 (the sensory-motor system), and the second half of Chapter 13 (the tactile and vestibular systems).

The principal goal of the book is to describe the computational structure and organization of the human brain. The theories presented here are, for the most part, mine although some have been improved by my students. Many of the ideas have been presented elsewhere as formal models, and several of them are included as appendixes to the appropriate chapters. Much of the material is new and under current investigation. For example, Scott Zimmerman and I are just now completing computer simulation studies of various parts of the movement control system discussed in Chapters 14 and 15, and Bryant Julstrom has just completed computer simulation studies of a model of parts of the spatial system, including spatial memory and the object buffers. We have not yet begun to simulate the body profile system described in Chapter 13, however.

The focus throughout this book is on information processing, but I will pay particular attention to information storage. Information storage is, after all, fundamental to virtually all intelligent activity. The first six chapters develop the theoretical framework needed for understanding the computational nature of the brain. Among the topics explored are the nature of information and the structures and functions of storage networks, information pathways, and information-encoding and transforming networks.

Chapter 1 describes the neuron, the basic computational element of the brain. Various properties of neurons are discussed, including the different logical operations they must perform and how they are organized into neural networks. The appendix to Chapter 1 presents a mathematical model for the neuron as a computational element.

Chapter 2 focuses on information and its characteristics. After all, neural networks store, transform, and transmit information, so an understanding of the nature of information is essential. Finally, several types of neural networks are introduced. These networks are components of many of the systems described later in the book.

Chapters 3 and 4 focus on information storage networks and their control. Chapter 3 describes the architecture of a typical associative storage network. It is described both in terms of its input, output and control functions and in terms of its internal organization: It is composed of numerous independent storage locations. The appendix to Chapter 3 presents a model for cortical storage.

Associative storage networks are crucial to brain function. Associative storage networks translate information from one representation to another. When we see a familiar object, we can name it. When we want to move a finger, we can move it. In the first case a visual representation is translated into a symbolic representation; in the second case a high-level intention is translated into a motor program. Both operations are performed by associative storage networks. Associative storage networks generate representations whose temporal characteristics are better suited to the next stage of processing than the previous representations. Phonemes vary rapidly as a function of time, words vary more slowly, ideas more slowly yet. Associative memory stores generate representations of phonemes from auditory patterns, representations of words from phoneme patterns, and representations of ideas from word patterns. While each representation varies more slowly than the previous one, it also lasts a lot longer. Each representation has vastly different temporal characteristics than the previous representation, which makes it more suitable for the next stage of processing. Chapter 5 lays the foundation for understanding these and other encoding and translating mechanisms.

Chapters 6 through 11 have a different flavor from the first five chapters. Whereas the first five chapters present issues of a conceptual or theoretical nature, Chapters 6 through 11 discuss particular sensory and storage systems and the representations they use.

Chapter 6 describes selected aspects of human memory and presents evidence that information is indeed stored by the human brain in storage systems of the type described in the previous chapters. It also shows that there are many different storage systems which differ from one another in structure, organization, function, trace permanence (immediate, temporary or permanent), trace time constants (rapidly varying to slowly varying) and pattern size (from a few elements to tens of millions of elements).

Chapters 7 through 9 focus on the visual system. Chapter 7 describes the low-level visual encodings and the networks which perform them. As you will see, the visual system extracts specific low-level features from the visual field and creates a set of storage representations which encode the world and objects in it. These storage representations use codes which enable the storage systems to

locate related stored information. Chapters 8 and 9 describe high-level visual representations, including storage representations of visual experience, representations of mental images, and representations of the world and objects in it. Chapter 9 focuses on the permanent visual storage systems and describes how visual experiences can be recognized and how memories of visual experiences can be mentally scanned.

Chapter 10 describes the auditory system and draws parallels between auditory and visual processes. The nature of stored auditory experiences is explored.

Chapter 11 presents an introduction to understanding. We understand an utterance, gesture, or situation when we know how to respond to it. That is, we understand when we are able to control our mental and physical apparatus to process all appropriate information, both current and stored, and decide what to do. (Understanding does not mean that we will respond, however.) Mental procedures are one high-level encoding of knowledge and I show in Chapter 11 that understanding means we recall from memory or generate a mental procedure which, when executed, appropriately controls our response to the situation. A final section briefly suggests the minimum computational circuitry needed for a system to learn to use natural language.

Chapter 12, the first chapter that deals with the control of movement, describes muscle tissue and the anatomy of the sensory-motor system. This chapter lays the foundation for understanding how high-level intentions control actions.

Chapters 13 through 15 have a notably different flavor from previous chapters and describe a framework for understanding the control of movement. The ideas presented in these chapters are under current investigation and lack many details. Nonetheless, enough details are presented to show in principle how we control movements.

Chapter 16 describes the affect system and suggests how affects influence high-level decisions. The neural networks that process affects are only beginning to be understood so this chapter serves to introduce affects and their relationship to purposive behavior. The computations that underlie decision making differ from those which underlie sensory and motor processing, and this chapter illustrates the nature of the differences.

The final chapter attempts to organize the material presented in the previous 16 chapters. Networks introduced earlier in the book are grouped into the sensory, symbolic, and purposive systems according to the types of information they process. The spatial system deals with space, objects, the body, and physical interactions between them, and it maintains all the representations used for recognizing and manipulating objects, navigating, controlling locomotion, and so forth. The symbolic system creates and processes symbolic information and is responsible for natural language processing (recognition and production of speech, writing, reading, etc.), mathematical and logical thought, planning,

and game-playing, to name a few. The purposive system makes all high-level decisions and ultimately controls itself and the spatial and symbolic systems. The purposive system includes the affect system which, when we are born, is controlled by innate (prewired) capabilities. All three systems work closely together for much of what we do, and some of the interactions between them are discussed. Finally, this chapter suggests how the brain learns to accept and process information. I conclude by reviewing Piaget's stages of cognitive development and relating them to the computational networks already described.

Although I have attempted to convey the computational nature of the human brain, in fact I have only laid the groundwork for that understanding. Almost nothing presented here is known for certain and our knowledge of the computational systems is just beginning to accumulate. When trying to understand how the brain works as a computer, and therefore how computations are implemented in neural circuitry, it is clear that we know very little. We know almost nothing about how the brain processes natural language, logical thought, musical thought, mathematical thought, concepts, or intuitions. We know almost nothing about how the brain encodes beliefs, dreams, hopes, desires, pleasure, pride, or self-esteem. We know almost nothing about how the brain generates plans. We know almost nothing about how the brain represents will, inclination, motive, purpose, or choice. Even with respect to sensory encoding, which is perhaps the best understood aspect of brain function, we are certain about almost nothing. We do not know how many different representations are generated and kept about the world or the objects in it. We do not know how physical properties of objects are represented. We do not know what types of coordinate systems the brain uses, nor do we know how it determines coordinates and uses them. We do not know how the brain translates between coordinate systems.

On the other hand, we are at least beginning to ask the right questions. We are beginning to understand how storage systems store, recognize, and recall information. We are beginning to understand the relationships between storage control, access control, and learning. We are beginning to understand how the low-level sensory networks create canonical representations for storage and what the organizations are within storage. We are beginning to understand the relationships between time and information encoding and modality. We are beginning to understand how recognition and perception occur. We will only understand human thought in general when we understand the underlying structures and representations used by the human brain, and this study is, I hope, a start in that direction.

Robert J. Baron

SUGGESTED READINGS

The following readings are of a general nature and are excellent sources for additional background information.

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1

NEURONS: THE COMPUTATIONAL CELLS OF BRAINS

INTRODUCTION

The fundamental assumption that underlies this entire presentation is that the brain is a computer. It is comprised of some hundred billion computational cells called **nerve cells** or **neurons**, which interact in a variety of ways. This chapter will focus on neurons and how they interact with one another.

The brain is highly structured, with its major anatomical connections specified genetically. Some connections appear to be regulated by sensory stimulation early in life, but the extent to which the brain's architecture is determined by sensory stimulation is only beginning to be understood. In any event, once the physical connections between neurons have been established, they appear to remain fixed for the life of the system.

NEURAL NETWORKS AND THEIR ANALYSIS

Neurons are organized into well-defined and highly structured computational networks called **neural networks**. Neural networks are the principal computational systems of the brain and there are many types, including receptor networks, encoding and decoding networks, storage networks, and control networks. Many of them have been studied anatomically and have a well-known structure or **architecture**, and many also have a well-understood computational role. It is more often the case, however, that the brain's computational networks, which are sometimes called "nuclei," "centers," or "bodies" by anatomists, have been studied anatomically with their specific computational role not yet being understood. In many cases, certain computational networks are predicted but their anatomical location and structure are not known.

Each neural network receives inputs through specific input pathways, process

them in a well-defined way, and responds to them through specific output pathways in a manner that depends on current and past inputs. The ultimate goal of this research is to understand all computational activity of the brain in terms of these constituent networks, how they interact with one another, and for receptor networks, how they react to the environment. We are a long way from achieving this goal.

There are many facets to understanding the human brain and its computations. At the most elemental level we seek to understand the mechanisms of the nerve cell. In time, neural interactions will be understood in terms of cell structure, metabolic activity, transport mechanisms, and so forth, and this level of understanding should lead to descriptions of the networks in which both the statistical properties of the nerve cells (spike train statistics) and the electrical activity (presynaptic and postsynaptic potentials, refractory periods, synaptic delays, axonal conduction, etc.) will be quantitatively related to the activities of other neurons and nonneural elements (notably glial cells) that make inputs to the networks. This level of understanding will not be discussed at any depth here.

At a somewhat less elemental level we seek to understand the **logical** interconnections of small groups of cells. We seek to understand their input-output or **computational** behavior in terms of the activities of their cells. This is the black box level of modeling, and there are two different methodologies for studying neural networks at this level. One is to select a particular biological network to study, model the structure and interactions of its neurons, and determine by suitable mathematical analysis or computer simulation how the model network behaves. The validity of the model is then checked by comparing its computed properties with the corresponding properties of the biological system as determined experimentally. This methodology is generally adopted by the theoretical biologist when modeling networks such as the nervous system of the crayfish, the eye of the cat, the retina of the frog, the olfactory bulb, and the cerebellum. A second methodology is to define the desired input-output properties of a network and determine what types of neural interactions and structures are required to realize the desired behavior. Within this methodology, experimental and anatomical considerations are generally used to constrain the models. This is the approach I have adopted for studying information processing in the brain, including learning, visual and auditory recognition, information storage and memory, natural language processing, the control of movement, and the affect systems.

The most general level at which one can study brain function is in terms of its component information-processing networks and interactions between them. Thus one may consider a system that contains a receptor network (retina, cochlea, etc.), information-transforming networks, memory stores, adaptive control networks, and so on, without considering in detail the underlying neural

activity. This is the system level of modeling. At this level of analysis one looks primarily at the psychological (behavioral) properties of the entire system in terms of its architecture—its functional components and their organization.

NEURONS

Since the primary concern throughout this book will be with the computational nature of the human brain, I will begin with an overview of the neuron and neural interactions. Two facts should temper this discussion. First, there is an enormous variety of neurons in the brain, with fundamental differences in morphology (structure), patterns of connections, and the way that neurons send and receive information. (See for example my discussions on the retina, the superior olive, and the cerebellum later in this book.) This discussion attempts to convey only those features that are common to most types of neurons—the average neuron, so to speak. Second, our current knowledge of neural interactions is limited in many respects, and although there is a large body of knowledge about certain aspects of neural interactions, other aspects are virtually unknown. This discussion describes only those aspects which are best understood.

A neuron consists of four parts essential to our understanding: the **cell body** or **soma**, **dendrites**, an **axon**, and **axon branches**, **collaterals**, or **terminal fibers**. See Figure 1.1. Dendrites are filamentous extensions of the soma which branch many times in the region surrounding the soma, forming the **dendrite tree**. The region in space occupied by the dendrite tree of a neuron is its **dendrite field**. The soma and dendrite tree are the receptors of signals from other neurons. A single axon originates at the soma, extends some distance, and divides often many times into a set of axon collaterals. The place on the soma where the axon originates is the **axon hillock**. Some axon collaterals progress to other parts of the brain where they divide even further before contacting other neurons. The regions in space occupied by the axon collaterals of a neuron are its **axon fields**. Each terminal fiber ends in a **synaptic button**, which almost contacts a dendrite branch or soma of another or the same neuron. Each such place of near-contact is called a **synapse**, and the space separating the two cells is called the **synaptic cleft**. See Figure 1.2. Synapses are essential for the information processing done by the neurons and will shortly be discussed in more detail.

A neuron normally maintains an ionic concentration gradient across its cell membrane, which produces an electric potential. When the membrane potential at the axon hillock is sufficiently disturbed, a self-sustaining **depolarization pulse** (sometimes called **impulse**, **pulse**, or **spike**) propagates along the axon and spreads throughout all axon collaterals. When the potential fluctuation caused by a depolarization pulse reaches a synapse, chemical transmitters are released. The chemical transmitters, which are ordinarily held in synaptic vesicles, are released and diffuse across the synaptic cleft to the cell membrane of the

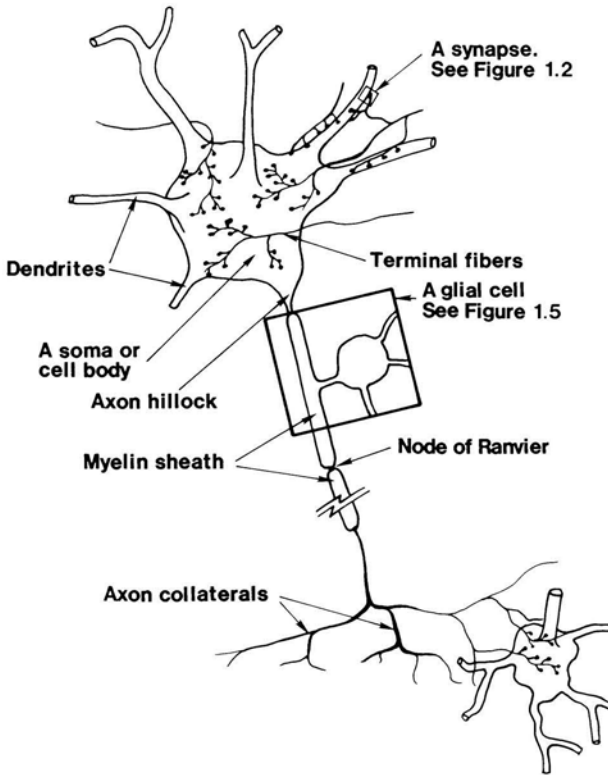


Figure 1.1 The structure of a typical neuron. Only a few of its synaptic contacts are shown.

postsynaptic neuron where they bind to receptor sites and may excite (tend to depolarize) or inhibit (tend to hyperpolarize) the postsynaptic cell. Within a short time after the chemical transmitters are released from the nerve endings, they are inactivated enzymatically, reabsorbed by the nerve terminals, or removed from the synaptic area by diffusion. The postsynaptic cell soon returns to its normal resting potential.

There are many different types of synapses as illustrated in Figure 1.3. Synapses of the type just described are axosomatic or axodendritic depending, on whether the contact is to a soma or dendrite. Axodendritic synapses may also terminate on specialized dendritic structures called dendritic spines, as illustrated at the top of the figure. Synapses between two axons are axoaxonic and those between two dendrites are dendrodendritic. Axosynaptic synapses, illustrated in the figure, are specialized structures often found in receptor networks; their intended computations are not yet understood. Finally, some synapses release chemical transmitters which control capillary constriction, muscle contraction (at structures

called motor end plates) or in some unknown way the extracellular medium. The latter class of synapses are axoextracellular or free endings.

The influence that the presynaptic neuron has on the firing of a postsynaptic neuron is not exerted at one synapse alone but through many synaptic contacts that are distributed over parts or all of the soma or dendrite tree of the latter. The morphology of a neuron and the geometry and distribution of the contacts between itself and other neurons depends on the particular neuron and varies greatly between neurons in different parts of the brain. Figure 1.4 illustrates a few of the hundreds of varieties of neurons that can be found. Nonetheless, when a presynaptic neuron fires, the depolarization pulse causes the release of chemical transmitters at each of the synaptic contacts that it reaches. In this way one presynaptic cell may simultaneously influence thousands and perhaps tens of thousands of different postsynaptic cells, or in some cases only a single cell. The neurotransmitters that are released at a single synapse cause a slight fluctuation in the membrane potential of the postsynaptic cell in the region immediately surrounding the synapse, and these individual fluctuations spread from each focus of excitation. When a fluctuation arrives at the soma of the postsynaptic cell, its influence combines with all other influences that arrive at the same time from other focuses of excitation and may be of sufficient strength to initiate a pulse in the axon of the cell.

Although some neurons are contacted by a single presynaptic cell, most are contacted by many and often thousands of different presynaptic cells at thousands

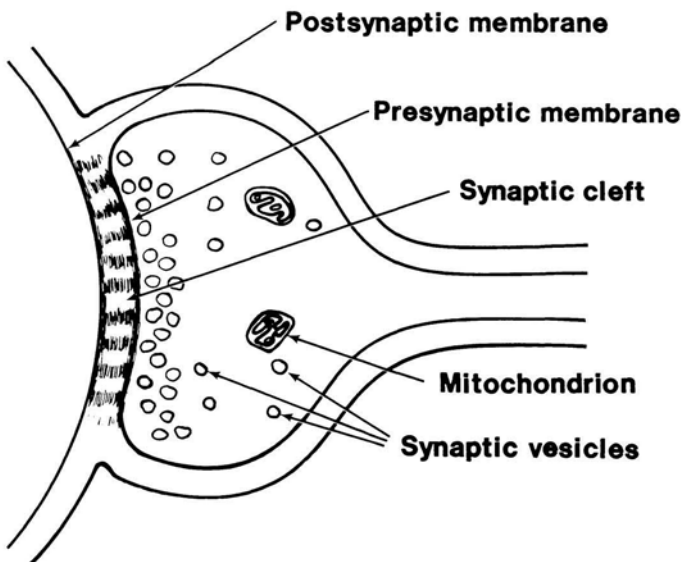


Figure 1.2. The structure of a synapse. (Mitochondria, found in most cells, serve as the center of intracellular enzyme activity.)

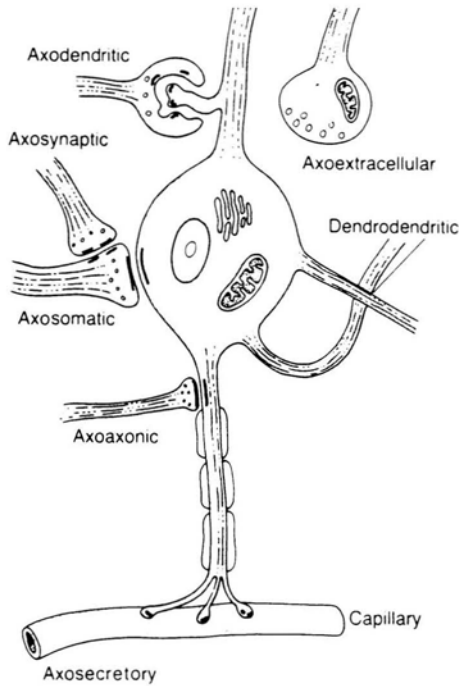
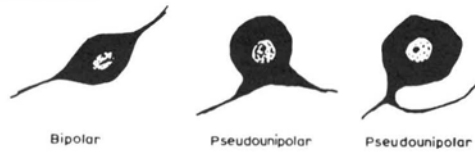


Figure 1.3 Different types of synapses. (Reproduced, with permission, from B. Kolb & I. Q. Whishaw, *Fundamentals of Human Neuropsychology*, 2d ed. © 1985 by W. H. Freeman and Co.)

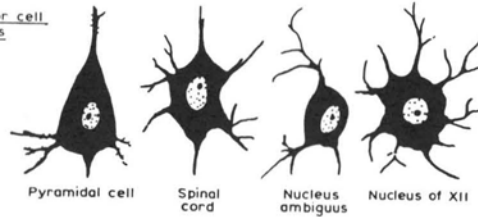
and perhaps tens of thousands of synapses. The fluctuations in the membrane potential at the soma, therefore, depend on the combined influence of all of the presynaptic cells. Furthermore, at a given synapse and at a particular moment of time, the effect of the neurotransmitters depends both on the quantity and type of neurotransmitter released. The magnitude of the resultant potential fluctuation in the postsynaptic cell also depends on the conductive properties of its dendrites, on the current state of the neuron's environment, on the current rate of cell metabolism, and on the presence of drugs, chemicals, and hormones which directly influence or regulate synaptic activity. At the present time there is not a single cell in a mammalian brain that is completely understood.

Although neurons are the logic elements of the brain, the brain consists of numerous other types of cells as well: blood vessels, connective and supporting tissue, and protective tissue. Within the brain, glial cells or glia occupy essentially all of the volume not occupied by neurons or blood vessels, and glia outnumber the nerve cells by an estimated 10 times. Glia provide both structural and metabolic support for the neurons and therefore directly influence neural activity. However, the way and the extent to which glia influence neural activity is not known in general.

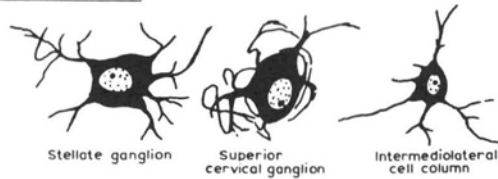
Sensory neurons



Motor cell types



Sympathetic neurons



Parasympathetic neurons

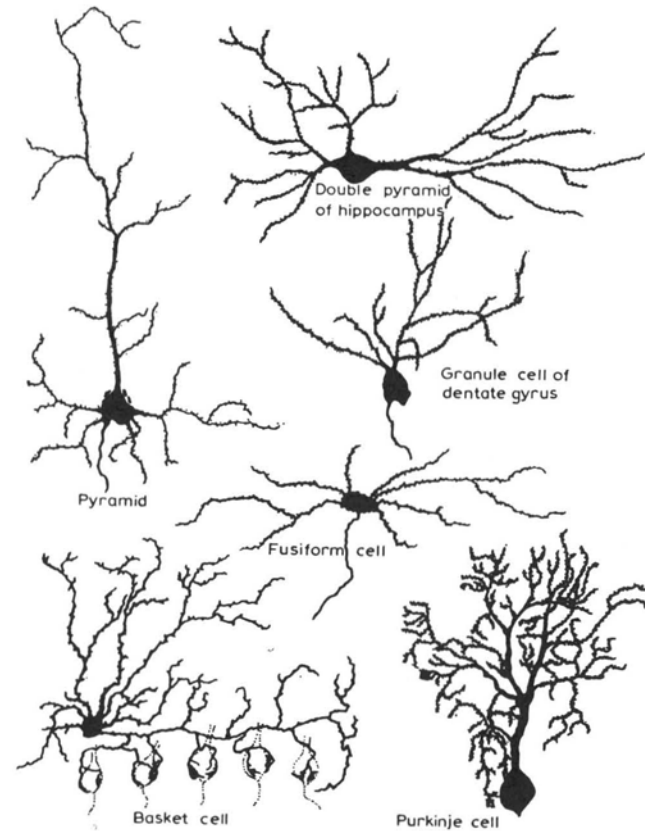
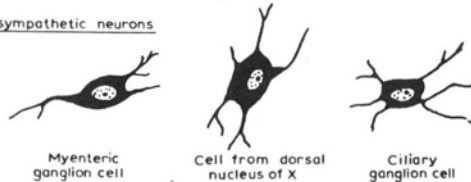


Figure 1.4 The appearance of the soma, dendrite tree, and axon ramifications of several types of neurons. (Reproduced, with permission, from J. P. Schadé & D.H. Ford, *Basic Neurology. An Introduction to the Structure and Function of the Nervous System*. © 1965 by Elsevier Biomedical Press.)

Perhaps the oldest known and best-understood aspect of neural activity is the mechanism by which the cell membranes of neurons conduct potential fluctuations. As described earlier, these fluctuations, which result from synaptic activity, propagate away from each focus of excitation. Neural membranes are semipermeable to sodium and potassium ions and act as a pump, removing sodium ions from within the cell while pumping potassium ions into the cell. The cell membrane cannot be penetrated by most other components of intracellular fluids. The result of the pumping action is a potential gradient across the cell membrane of about 70 millivolts, negative inside the cell and positive outside. This is the cell's resting potential. A potential fluctuation at one region of the cell's membrane triggers a change in the conductance of neighboring regions to sodium and potassium ions. The stimulus trigger for the changing conductance is local current flow in the cell's membrane induced by the potential fluctuation. Sodium ions are first allowed to rush into the cell. This changes the membrane potential from approximately -70 millivolts to approximately $+40$ millivolts. A moment later potassium ions are allowed to rush out. The efflux of potassium ions restores the resting potential of the cell. After that, the cell membrane slowly expels the sodium ions and restores the potassium ions until the membrane once again reaches its resting potential.

For the axon of most neurons the situation is somewhat different. Most axons are surrounded by an insulating sheath of myelin, which is a sheet-like extension of one type of glial cell known as an oligodendrocyte. See Figure 1.5. The myelin sheath partly isolates the axon from the normal concentrations of ions found in most extracellular space and prevents the local currents from forming in the neural membrane. In fact, the potential fluctuation propagating into an axon would disappear entirely if it were not for one important fact. The myelin sheath is not continuous along the entire length of the axon but is interrupted every millimeter or so by a break called a node of Ranvier. The nodes of Ranvier are the gaps between myelin supplied by different glial cells. The only currents that can form pass through the nodes of Ranvier, and as a consequence, the potential fluctuations, the pulses, jump from node to node. Conduction in myelinated axons is called saltatory. A pulse entering one end of a myelinated axon essentially "jumps" from node to node until it reaches the other end of the axon, where the myelin sheath is no longer present. At that point the potential fluctuation is at its full strength. This accounts for the all-or-none conductive property of myelinated axons and enables one to characterize a nerve cell as "firing" or "conducting a pulse." The **rate of firing** of a cell is limited to about 1000 pulses per second because of the time constants of the underlying mechanism. Based on the all-or-none conductive property of axons, the firing rate of a neuron is taken to be the number of times its axon conducts a pulse per unit of time. Researchers often refer to spike train statistics when characterizing neural activity in this way.

In the peripheral nervous system, Schwann cells form the myelin sheaths around axons as shown in Figure 1.6.

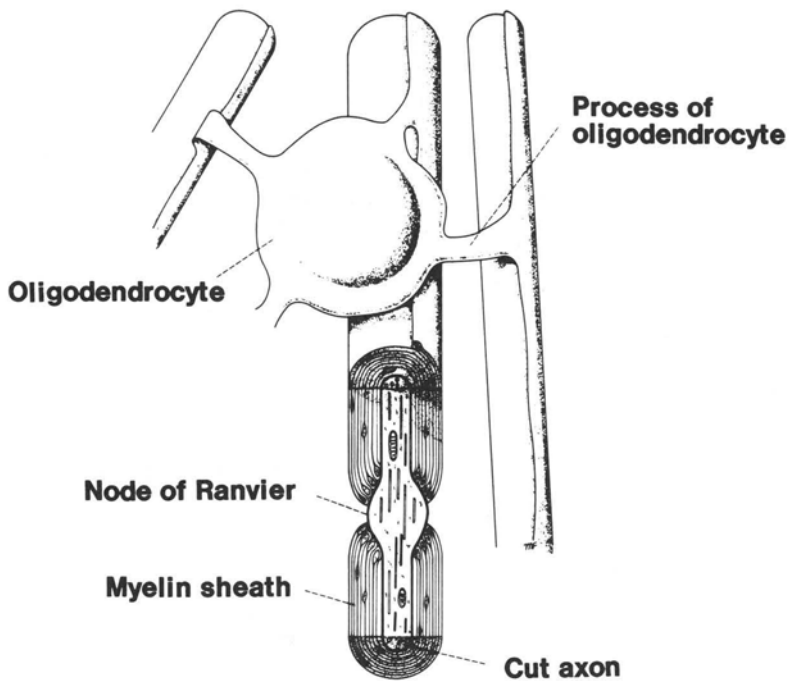


Figure 1.5 An oligodendrocyte is one type of glial cell. The processes of the cell illustrated here form the myelin sheaths surrounding the axons of four different neurons of the central nervous system. The separations along an axon where two glial cells almost contact each other are the nodes of Ranvier. (Reproduced, with permission, from R. S. Snell, *Clinical Neuroanatomy for Medical Students*. © 1980 by Little, Brown, and Co.)

In summary, a neuron transmits information to other neurons along its axon in an all-or-none fashion. Depolarization pulses are generated at the soma, propagate along the axon and all collaterals, and release neurotransmitters which cause perturbations in the resting potentials of all postsynaptic cells. These cells integrate the effects of all arriving potential fluctuations and fire accordingly.

OTHER TYPES OF NEURAL ACTIVITY

Nonspiking Neurons

The “spiking” or “depolarization” of a neuron is generally associated with axonal conduction in myelinated axons. Keep in mind, however, the fact that the membrane potential of every neuron is in a constant state of fluctuation, and it is the fluctuation in membrane potential at a synapse, if sufficiently strong, that initiates the release of chemical transmitters. In line with this, some cells,

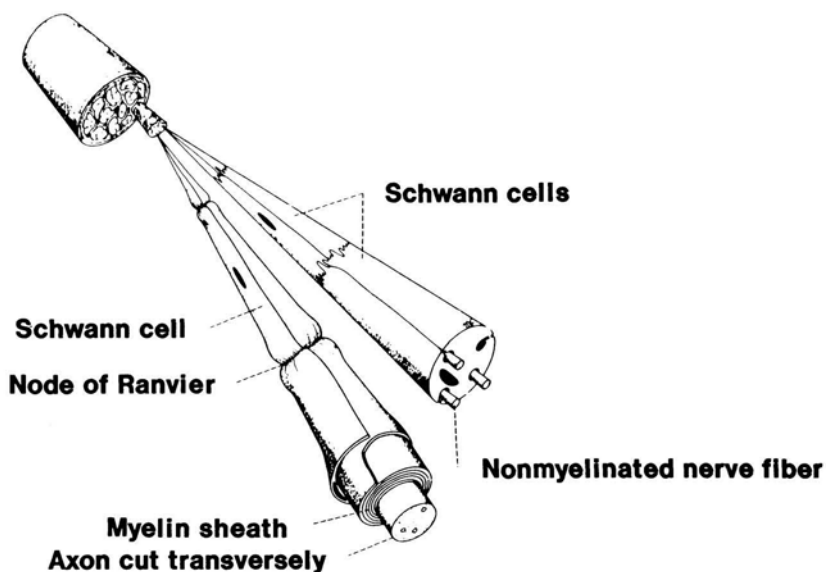


Figure 1.6 Schwann cells form the myelin sheaths of axons of nerve cells in the peripheral nervous system. (Reproduced, with permission, from R. S. Snell, *Clinical Neuroanatomy for Medical Students*. © 1980 by Little, Brown, and Co.)

notably certain receptor cells, do not spike at all and in fact do not have axons. Information is conveyed from these nonspiking neurons to other cells through synaptic contacts that occur between cell bodies or cell body and dendrites. The fluctuations in a nonspiking cell cause corresponding fluctuations in the resting potential of the postsynaptic cell, which may in turn generate spikes in its axon. Nonspiking cells are highly specialized and have developed for specific information-processing tasks.

Chemoemissive Neurons

The synaptic contact, although by far the most prominent and best understood, is not the only type of information transfer between cells. Some neurons emit different types of molecules which affect the transmissive properties of all nearby cells. These nonspecific contacts have not been extensively studied, but the need for nonspecific information transfer, particularly to support various control processes, will become apparent in this and later chapters.

Logical Categories of Cells

For purposes of understanding the logic of neural networks it is convenient to define several logical categories of neurons. **Information input neurons** deliver information to a network for processing or analysis, and **information output**

neurons deliver processed information from a network to another. The output from one network is logically the input to another. For example, the optic nerve delivers the output from the retina and therefore consists of output cells. However, the optic nerve terminates in the lateral geniculate nuclei within the brain and therefore consists of input cells to those networks.

Control cells regulate the processing done by a network. The control inputs to one network may be the information outputs from another network.

A cell that is self-excitatory may be **bistable**. A cell is bistable if, when stimulated by other cells to an adequately high firing rate, its self-excitation will keep it firing indefinitely until turned off by an inhibitory input. If it is not firing, however, it remains off until it is stimulated by other cells. Such a cell is either **active** or **inactive**. The minimum firing rate that is required to activate an inactive bistable cell is its **threshold firing rate**. By analogy, an ordinary light switch can be lightly pushed without causing the switch to switch, but when pushed hard enough—beyond its threshold—it snaps and the light turns on or off. The switch is stable either in the “on” position or the “off” position; hence it is a bistable device.

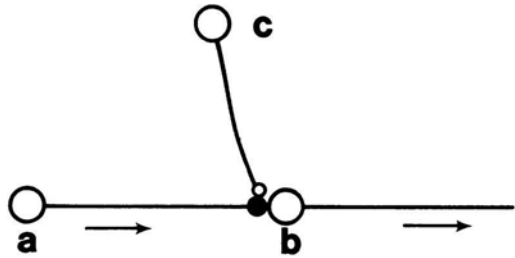
When a single control cell is used to initiate activity in a network, that control cell is a **command cell**. If, for example, a single cell is used to initiate recall from a memory store, then that cell is a command cell. However, activity in a command cell may not be sufficient to initiate the action that it controls. Again by analogy, the playback button on an ordinary tape recorder is a command button. However, when the power is turned off or the batteries are removed, the playback button does not initiate playback.

Logical Categories of Neural Interactions

Different neurochemicals, such as neurotransmitters, peptides, enzymes, or pathological agents, influence neural transmission in a variety of ways. Inhibitors of biosynthesis prevent neurotransmitters from forming. Presynaptic blocking agents inhibit the release of transmitters at the presynaptic membrane. Presynaptic facilitators have the opposite effect. Postsynaptic blocking agents bind to receptor sites at the postsynaptic membrane preventing ordinary transmitters from doing so. This blocks their activity. Mimicking agents act as neurotransmitters, causing depolarization or hyperpolarization of the postsynaptic cell, depending on the type of mimicking agent. Some chemicals inhibit metabolic breakdown of the transmitters while others block their reuptake by the presynaptic cell. Still other chemicals alter the conductance of the cell membrane, thereby changing its transmission properties. Moreover, the affect that a particular chemical agent has depends on the normal neurotransmitter of the synapse. See, for example, Arnold (1984) for a detailed discussion and references to the literature.

Different neural networks perform markedly different information-processing

Figure 1.7 Two idealized neurons, a and b, which have uniform coupling regulated by neuron c.



tasks, and the variety of requirements imposed on them accounts for the large variety of mechanisms employed by the neurons themselves in their underlying computations. Some networks simply route information from one place to another. This implies a mechanism for blocking the transmission of all information along a pathway. Networks which block transmission must act as switches and have a very fast switching time. In contrast, some networks transform information in a variety of subtle ways. Visual networks which enhance the retinal image, for example, must transform their patterns in much the same way that the contrast knob on a television set enhances the image. Although we do not yet know what types of neural activity are used to support any given information-processing task, and we are in fact only beginning to understand the range of computational demands made on the brain; still, the following sections suggest some of the expected types of coupling needed by the brain to meet these demands. Only when researchers specifically begin to look for these and other logical systems will we discover which ones exist.

Regulatory Coupling. Neurons whose activity regulates the activity of other cells are connected by **regulatory coupling**. Figures 1.7 and 1.8 each illustrate three idealized cells, A, B, and C. In Figure 1.7, cells A and B have uniform coupling, and cell C is a control cell with **negative regulatory coupling**. When control cell C fires, the normal coupling between cells A and B, whether it be excitatory or inhibitory, is reduced so that cell A makes a smaller contribution to the firing rate of cell B. If cell C fires fast enough, then cell A makes no contribution to the firing rate of cell B. When cell C does not fire, cell A is connected to cell B as described earlier. Cell C **regulates** the coupling between cells A and B by blocking their interaction and is said to have a **negative regulatory effect**. **Positive regulatory coupling** is defined analogously and facilitates the inhibitory and excitatory coupling between cells. In Figure 1.8, cells A and B have regional coupling, and cell C is again a control cell having negative regulatory coupling. When cell C fires, the coupling from cell A to cell B is reduced or blocked, but only in that region influenced by cell C. Coupling elsewhere between cells A and B is unmodified by the firing of cell C.

Transformational Coupling. In contrast to neurons which regulate the activity of other neurons, those which are connected together to process information use either **excitatory** or **inhibitory** coupling. Figure 1.9 shows a simple network having three sets of cells, I, C, and O. The collection named I is the input set, collection C is the control set, and collection O is the output set. A **neural network model** for the illustrated network consists of a complete and precise specification of the activity of each output cell when given the activity of each input and control cell for all time up to the present, and a complete specification of the state of each neuron's environment. For a biological network, a partial list of parameters needed for determining the firing rate of each output cell at time t is the following:

1. The structure of each output cell, including its size and the distribution of synaptic contacts from all presynaptic cells.
2. The rate of firing of each presynaptic cell.
3. The rate of release of neurotransmitters from each presynaptic cell as a function of its rate of firing, the current state of the neurons' environment, the effects of the control inputs on the release of neurotransmitters, and the history of all inputs to the network.

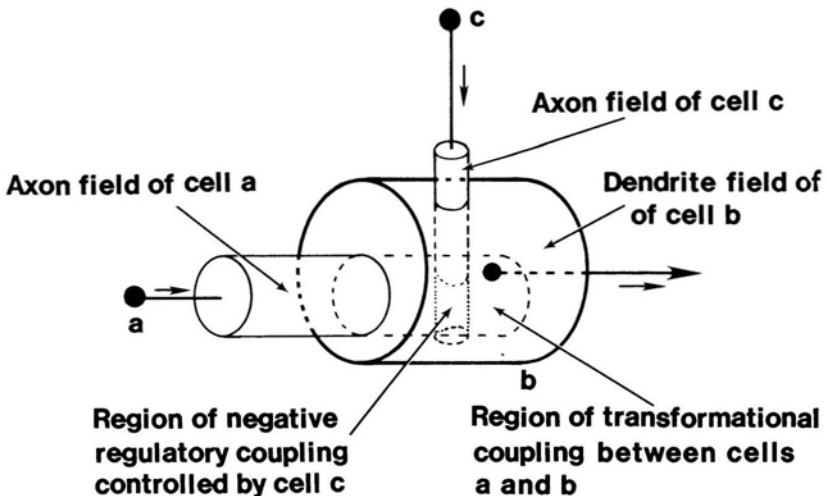
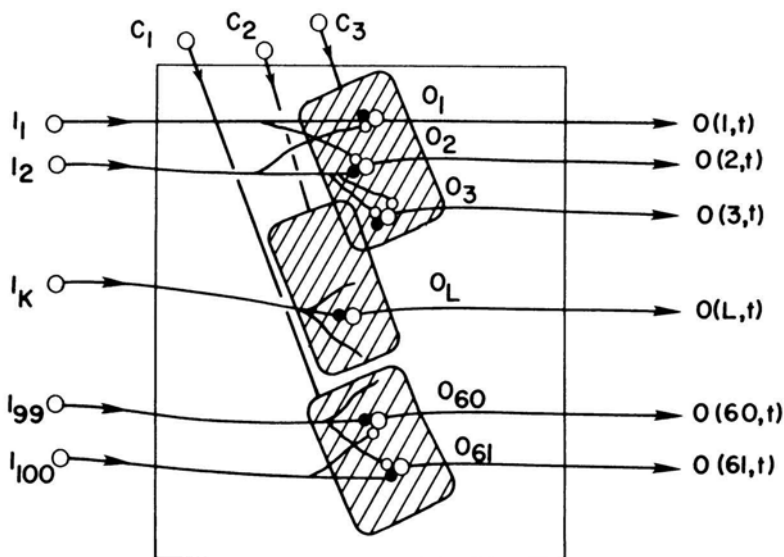


Figure 1.8 Two idealized neurons, a and b, whose coupling is regulated by neuron c. Transformational coupling occurs between neurons a and b within the volume enclosed by the larger intersecting cylinders. Control neuron c regulates the coupling between neurons a and b only within the volume enclosed by the smallest cylinder. Control neuron c also regulates the coupling between all other transformational neurons connected within that volume.



Symbolic diagram

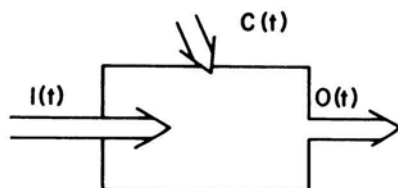


Figure 1.9 A simple neural network composed of 100 input neurons, 3 control neurons and 61 output neurons.

4. The influence that the current state of each neuron's environment has on the movement of neurotransmitters from presynaptic to postsynaptic cells.
5. Any mutual influences that neurotransmitters released by different presynaptic cells have on one another.
6. The sensitivity at the current time of the postsynaptic cell toward depolarization (or hyperpolarization) due to the arrival of neurotransmitters, and any modification to that sensitivity due to the current state of its environment.
7. The influence that the current state of each neuron's environment has on its depolarization.

As the above list suggests, the influence that the presynaptic cells have on the firing rate of a postsynaptic cell is only one part of the interaction between cells. We call this component the **transformational coupling** between cells. In either

case, if one cell tends to cause another cell to discharge it is excitatory and if it tends to prevent another cell from discharging it is inhibitory. Transformational coupling determines the type of processing performed and is distinguished from control coupling, which regulates the transformation, and effectual coupling (to be described next) which initiates or effects a temporary or permanent change in coupling.

Effectual Coupling. The third and final type of neural coupling to be considered is effectual coupling. An input to a network is an **effectual input** and has **effectual coupling** in case its firing causes or initiates either temporary or permanent changes to take place in the transformational coupling characteristics of other cells. This differs from control coupling in that the changes do not directly affect neural transmission. Furthermore, the changes may persist after the effective neurotransmitters are no longer present. A neuron that initiates the consolidation process in a storage network makes an effectual input to that network. A neuron which makes an effectual input to one network may also make regulatory or transformational inputs to the same or other networks.

SUMMARY

The three types of coupling described here, regulatory, transformational, and effectual, are only beginning to be understood. From a logical point of view, all three types of coupling are necessary. However, the differences between control coupling and transformational coupling, for example, depend on the computational logic of networks, and the computational logic cannot be determined without knowing exactly what functional role the various neurons play in the computational process. Since computational roles are just beginning to be understood, these notions will become increasingly important as time passes. The relationship between cell morphology and its computational role will someday be understood, and when that happens, I expect researchers will find a direct relationship between cell morphology, coupling type, and coupling characteristics.

It should be clear that any attempt to formulate a complete and detailed model of the brain is, at the present time, impossible. We simply don't have enough quantitative information about the interactions between neurons to do so, and even if we did, the computational difficulties of specifying the activities of some hundred billion neurons with perhaps one hundred trillion synapses, their environment, and the entire history of inputs to the system is simply not computationally feasible. This, then, would be the end of this endeavor except for one very important fact. We know a lot about the computational processes of the brain. We know that representations of visual images are processed, that records are made of our experiences, that we manipulate mental models of the

world, that we communicate with one another using natural language, that we can perform numerous types of logical computations, that we have emotional experiences, and that we control our own movements. Our way out of the dilemma of attempting to model the brain by studying its individual neurons, then, is to build various computational networks which perform the same processes that occur in the brain, and use those neural network models as a guide to understanding the computational logic of the brain. The neural network models are constructed out of neuron-like elements called mathematical or abstract neurons, and by using our knowledge about the structure and function of the human brain we can build those models to resemble the networks of the brain closely. As our understanding of the brain increases, the models will be refined and approximate more closely the corresponding networks of the brain. This, then, will be the strategy followed throughout this endeavor.

SUGGESTED READINGS

The following excellent references are among many that present the biological ideas which motivated this chapter.

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APPENDIX 1 THE MATHEMATICS OF NEURAL INTERACTIONS¹

This final section presents a formal model for neural interactions. The material is not essential to the remainder of the book and the reader may wish to proceed directly to Chapter 2.

¹This material is reproduced, in part, from R. J. Baron (1970) A model for cortical memory, *Journal of Mathematical Psychology*, 7, 37–59.

As I suggested above, the model presented here describes the logical interactions between neurons and is an approximate description for the interactions between biological neurons. The model relates the output behavior of a network of abstract neurons to the behavior of the input and control neurons to that network. The model is linear and assumes statistical interactions between neurons.

When discussing different collections of neurons, either biological or mathematical, it is convenient to name them. For example, the retinal ganglion cells may be named RG whereas the cells of the olfactory bulb may be named OB. In order to distinguish one cell from another in a particular collection, we will enclose in parentheses a list of numbers which uniquely identify a particular cell in the collection. These are the **intrinsic coordinates** of the cell. If the collection is two-dimensional, then two number positions will be used, where the numbers in each position specify (in arbitrary units) the location of the cell in the collection. For example, the retinal ganglion cells may be designated RG(1,1), RG(1,2), RG(1,3) . . . RG(2,1), RG(2,2) . . . RG(M,1), RG(M,2) . . . RG(M,N), where M and N are the maximum number of cells in the two dimensions under consideration. If the collection is one-dimensional, then a single number position will be used, and if the collection is three-dimensional, then three number positions will be used. This notation clearly generalizes to any number of dimensions. When we wish to designate an entire collection only the name will be used and it will be set in boldface type.

If the coupling parameters between cells depend in a systematic way on the cell's intrinsic coordinates, then the network has **high neural specificity**. On the other hand, if the coupling parameters do not depend on intrinsic coordinates, the network has **low neural specificity**. The cells of a network having random coupling coefficients would have low specificity. If each cell on the retina is computationally distinguished by its position, then there would be a functional relationship between its cell number and its position on the retina and the retina would have high neural specificity. You will see that the human brain has high neural specificity. It is generally assumed that cell morphology and network architecture are genetically specified. Coupling parameters may not be genetically specified, depending on the specific network.

We define a **mathematical neuron** (hereafter called simply "neuron") as consisting of four parts: (1) a **soma**, (2) a **dendrite field**, (3) an **axon**, and (4) an **axon field**. The soma is a point whose geometric coordinates identify the neuron. The dendrite field is a three-dimensional volume containing the soma. The axon field is also a three-dimensional volume (not necessarily disjoint from the dendrite field), and the axon is a line connecting the soma with the axon field. See Figure 1.10.

When the axon field of one neuron, the **presynaptic neuron**, intersects the dendrite field of a second neuron, the **postsynaptic neuron**, the intersection is

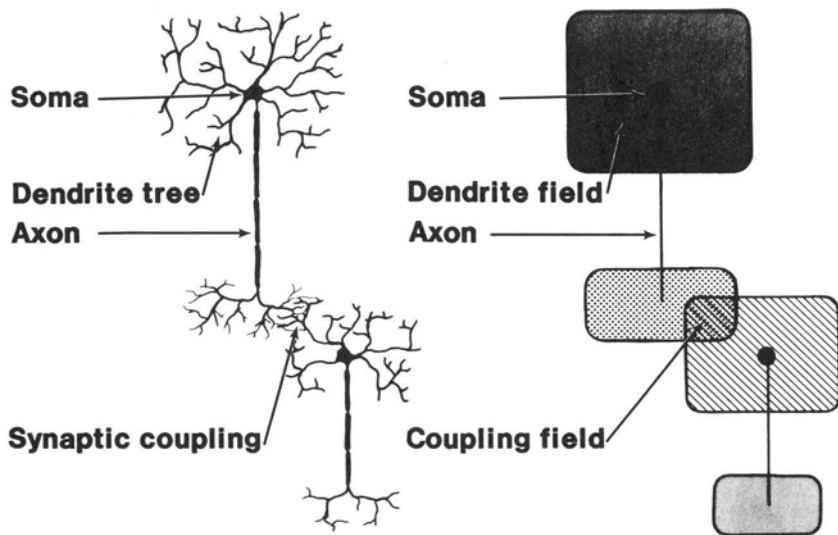


Figure 1.10 The relationship between biological neurons and mathematical neurons. (Adapted from R. J. Baron, A model for cortical memory. *Journal of Mathematical Psychology*, 7, 1970, 37-59.

called the **coupling field**. The coupling may be transformational, control, or effectual. Consider two neurons with nonempty coupling field. Neuron A, the **presynaptic neuron**, is said to **synapse on** neuron B, the **postsynaptic neuron**.

The **frequency** of a neuron is a nonnegative valued function of time, as illustrated in Figure 1.11. Let I be a collection of input neurons, O be a collection of output neurons, and C be a collection of control neurons as illustrated in Figure 1.9. Let $I(J)(t)$ denote the frequency of cell $I(J)$ at time t and similarly let $O(K)(t)$ and $C(M)(t)$ designate the frequencies of cells $O(K)$ and $C(M)$ at time t .

Finally, let $E(x,y,z)(t)$ designate the **state** of the neural environment at time t and at geometric location (x,y,z) . We say that the neural environment is in a **normal state** in case $E(x,y,z)(t)$ has value 1.

When the neural environment is in the normal state and neuron $I(J)$ fires at frequency $I(J)(t)$, neuron $I(J)$ releases **transmitter substance** to neuron $O(K)$ throughout their coupling field at a rate density (quantity of transmitter substance per second per volume) given by

$$I(J)(t)c_{O(K)}^{I(J)}(x,y,z,C(t))$$

The parameters

$$c_{O(K)}^{I(J)}(x,y,z,C(t))$$

are called **coupling coefficients**, where the superscript identifies the presynaptic neuron and the subscript identifies the postsynaptic neuron. As indicated, the coupling depends on pre- and postsynaptic neurons and on the control input $C(t)$ to the region of coupling (x,y,z) . **Excitatory coupling** is represented by positive coupling coefficients, and **inhibitory coupling** is represented by negative coupling coefficients.

When the neural environment is not in the normal state it may influence the coupling between two neurons multiplicatively. Thus the rate of arrival of transmitter substance at $O(K)$ from $I(J)$ is given by

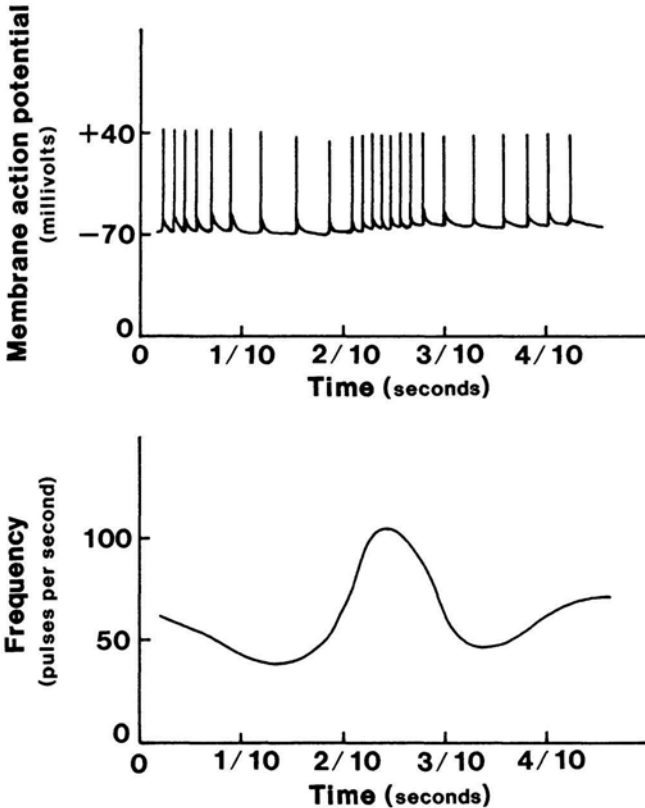


Figure 1.11 The relationship between the depolarization rate of a biological neuron and the frequency of a mathematical neuron. (Reproduced, with permission, from R. J. Baron, A model for cortical memory. *Journal of Mathematical Psychology*, 7, 1970, 37-59.)

$$I(J)(t)c_{O(K)}^{I(J)}(x,y,z,C(t))E(x,y,z)(t).$$

Since $E(x,y,z)(t)$ is 1 when the state of the neural environment is normal, this same expression is valid in general.

The axon and soma of our mathematical neuron do not play a central part in the model. Transmitter substance which arrives at the dendrite field of one neuron causes it to fire at a frequency given by integrating all contributions of transmitter substance which arrive throughout its dendrite field. However, the sensitivity of the postsynaptic cell to transmitter substances may not be uniform throughout its dendrite field. In any volume of the postsynaptic cell $O(K)$, the net rate density of arriving transmitter substance is given by

$$(\sum_{I(J)} I(J)(t)c_{O(K)}^{I(J)}(x,y,z,C(t))) E(x,y,z)(t)$$

where summation is over all neurons whose axon fields intersect the dendrite field of the postsynaptic neuron. The contribution toward depolarization of the postsynaptic cell may be modified by its **local sensitivity**, $k_{O(K)}(x,y,z)(t)$, at position (x,y,z) . The contribution toward the frequency of the postsynaptic cell made by the arrival of transmitter substance at point (x,y,z) in its dendrite field is given by

$$k_{O(K)}(x,y,z)(t) (\sum_{I(J)} I(J)(t)c_{O(K)}^{I(J)}(x,y,z,C(t))) E(x,y,z)(t)$$

The frequency of neuron $O(M)$ is given by integrating all such contributions over its entire dendrite field. The final result is given by

$$O(M)(t) = \text{POS}(\iint\limits_{\text{field}} k_{O(K)}(x,y,z)(t)(\sum_{I(J)} I(J)(t)c_{O(K)}^{I(J)}(x,y,z,C(t))) E(x,y,z)(t) dx dy dz).$$

The function $\text{POS}(x)$ has value x if x is non-negative and zero otherwise. That is, cell $O(M)$ does not fire if the net effect of all arriving transmitter substance is negative.

DISCUSSION

The equation given above represents a mathematical model for the logical interactions between neurons in a neural network. In particular, it relates the output firing pattern $O(t)$ to the input pattern $I(t)$ and the control pattern $C(t)$. Once all parameters are specified, the frequency of each output cell can, in principle at least, be determined.

A few comments are in order. First, this model is statistical and does not take into account relative phases between spikes arriving from different presynaptic neurons. Second, the model is linear: All effects contribute linearly to the frequencies of the postsynaptic cells.

Perhaps more important are the biological counterparts of the various coupling contributions. Coupling contributions come from three places: presynaptic (the c 's), interneuronal (the E 's) and postsynaptic (the k 's). The coupling coefficients (the c 's) depend on the intrinsic coordinates of the pre- and postsynaptic cell, the position of contact, and any effects that the control patterns have on the coupling. This model therefore assumes that control inputs regulate the presynaptic release of transmitter substance rather than the interneuronal or postsynaptic parameters. The neural environment (the E 's) contributes in a similar way to the coupling between all cells occupying the same volume of the network. Thus the environmental contribution is nonspecific. Finally, the postsynaptic neuron can also modify the coupling influence, and the postsynaptic cell's contribution (the k 's) may vary as a function of position on the postsynaptic cell. When creating a specific neural network model, it is essential to assign values to the appropriate parameters in the equations, depending on the assumed origin of the contribution.

Notice that effective coupling has not been included in the equation. Effective coupling modifies coupling parameters and can be directly incorporated either in the definition of the coupling coefficients or the definition of the local sensitivity values, whichever is appropriate. For the storage model described in Appendix 2, the effective inputs determine when and where storage will take place and are the "store now" signals to the storage system. Storage in that model consists of establishing values for the local sensitivity values (the k 's) of certain storage cells. In particular, the k 's take on one set of values before storage and a different set of values after storage. The effective inputs to a storage location determine *when* the k 's change values but have no other effect on the input-output relationships in the model.

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2

INFORMATION: ITS MOVEMENT AND TRANSFORMATION

INTRODUCTION

Many functions of the brain are similar to those of a modern digital computer. Both the brain and a computer accept information as input and produce information as output. Both encode and decode information. Both transform information in a variety of ways. Both store, search for and recall information. This chapter attempts to characterize information, how it is encoded, how it is transformed, and how it is transmitted from one place to another.

Information will be used here to mean two different things: (1) the pattern, arrangement, or configuration of constituent units that encode knowledge of form or event, and, (2) the signal impressed upon the input of a system and used to communicate knowledge of form or event. When used to encode knowledge, information is **static**; when used to communicate knowledge, it is **dynamic**. The terms static information pattern and dynamic information pattern, and static pattern and dynamic pattern will also be used.

STATIC AND DYNAMIC PATTERNS

Static patterns are the encoding of stored knowledge. The ink patterns on a page of text, the patterns of magnetic domains on a strip of recording tape, the grooves on phonograph records, the silver particles on a photograph, and the raised dots in braille are examples of static information patterns.

Dynamic patterns move or transmit knowledge from one place to another and interact with information-processing systems by supplying the energy needed to initiate information-processing operations. Light waves that convey printed information, electric signals generated by a playback head in a tape recorder, sound waves of speech, and firing patterns in collections of neurons are examples of dynamic information patterns.

Static patterns remain fixed in their supporting medium until modulated by an external activator; dynamic patterns, in contrast, are spatio-temporal patterns that exist because of a change in their supporting medium—an electric signal, a light wave, a mechanical movement. Static patterns are useless until converted into dynamic patterns: a book in the dark, a reel of magnetic tape with no tape deck, a phonograph record with no record player. The static patterns in these devices remains static, hence useless, without an appropriate playback mechanism. Once converted, however, static patterns are the source of all prior knowledge. When light shines on the printed page, when the magnetic tape is moved across a playback head, or when the grooves of a phonograph record move the stylus of a phonograph cartridge—these processes recreate the dynamic patterns that were originally present and stored when the static patterns were formed, and the recreated dynamic patterns once again become available for further processing and analysis.

For the printed page, the presence of a uniform external light source is necessary to convert from static to dynamic pattern; for a magnetic tape, the uniform movement of the tape across the playback head, and for the phonograph record the uniform movement of the record under the playback cartridge. Uniform light, uniform tape movement, and uniform record movement—these are the external modulators necessary for converting static patterns into dynamic information patterns.

Within the brain the dynamic patterns are the patterns of discharging neurons which convey signals from one network to another; the static patterns are the memory traces which are encoded as spatial patterns of biochemical markers. Chapter 3 will discuss information storage in detail, but for now let us take as self-evident the importance of static and dynamic patterns to brain function and continue to explore other facets of information.

CONTROL AND CONTENT PATTERNS

Information patterns can be loosely divided into two categories: **control patterns**, and **content patterns**. Consider a tape recorder that has three different recording channels. Two of the channels are used just as they are on any home stereo tape recorder: Each channel records a representation of the sound that arrives at a recording microphone in one part of the room. This tape recorder, however, has special circuitry that monitors the sound level in the room. If the sound level in the room increases during the recording session, the recording level of the two stereo channels is decreased. If the sound level decreases, the recording level is increased. (This optimizes the signal-to-noise ratio on the recording and enables a greater dynamic range without saturating the tape.) The third channel maintains a record of the recording level of the two stereo channels. If a tape consisting of just the two stereo channels is played back on

an ordinary tape recorder, the average sound level during playback would remain constant even though the sound level during the recording session varied. However, on the special recorder being described, the information stored on the third channel is used in a special way during playback. If the recording level was reduced during the recording session, then the volume is increased during playback so the sound level in the room is the same as it was during recording. Similarly, if the recording level was increased during recording, then the sound level is decreased during playback. The information recorded on the third recording channel is **control information**, whereas the information recorded on the two stereo channels is **content information**. The control information is necessary for the proper operation of the tape recorder, whereas the content information plays no direct role in its operation. Control information relates to the circuitry—it controls a process; content information relates only to the quality of the information being processed.

Notice that from the point of view of the recording circuitry there is no difference between the content patterns and the control pattern. In fact, all three patterns are stored and played back in exactly the same way. The pattern stored by the third channel only becomes control information when used by the playback mechanism. *It is how information is used that distinguishes content from control information, not the format of the information itself.*

Notice also that information only becomes meaningful when it interacts with a system that can correctly interpret it. The control information stored on the third channel of the special tape recorder is only useful to that recorder. A book written in Chinese is only useful to a person who reads Chinese. *Information only has meaning to a system that is designed to interact with it properly.*

INFORMATION TRANSMISSION

There are many different ways that information can be transmitted. In computers, for example, numerical quantities are transmitted as electrical signals on collections of wires. For a given wire, a signal can either be present or absent. For a single wire at a given time, the presence or absence of a signal encodes either the value one (signal present) or the value zero (signal absent). Likewise, the presence or absence of signals on N wires can be used to encode up to 2^N different values. For example, for two wires, if '00' indicates that neither wire has a signal, '10' indicates that wire 1 has a signal, '01' indicates that wire 2 has a signal, and '11' indicates that both wires have signals, then clearly all possibilities are exhausted. There are two wires and 2^2 or four different patterns. In each case, the pattern is dynamic since the electrical signals can directly interact with other computing devices which may be connected to the wires.

It is also possible to send time-varying dynamic patterns along wires. The

electrical impulses along a telephone wire are one example. As a second example, consider the very simple case of one wire, and suppose that the presence or absence of an electrical signal is inspected every second. If we inspect the wire N times during a period of N seconds, then up to 2^N different sequences of on and off signals can be sent along the wire. In a collection of M wires, up to 2^{MN} different sequences of signals can be sent.

Within computers, information is transmitted from one component to another along **data buses**. Data buses are simply collections of independent wires, one for each component of the information being transmitted. When a signal is impressed on one end of a wire, it can be sensed almost immediately at the other. When one computer component is to transmit information to another component, it places signals on the wires of a data bus. In some cases a single signal is sent but in other cases a sequence of signals is sent and the receiving circuits must inspect the data bus at exactly the correct times to discover what the sequence is. In general, because of the critical timing involved, all components of a computer are controlled by a **master clock**, a circuit that periodically turns on and off a clock signal in a special control wire that goes to all components of the computer to coordinate their activity. The individual components use this clock signal to determine when to place data on the data bus and when to inspect the data bus.

INFORMATION ENCODING

In computers, static information patterns are encoded in many different formats but most often as the pattern of “on” and “off” **states** in sets of storage elements. The fundamental storage element of a modern computer is the **flip-flop**, an electronic switch that is either “set” (on) or “reset” (off). A **set** flip-flop holds the value ‘1’ and a **reset** flip-flop holds the value ‘0.’ This is analogous to a light switch which can either be on or off. Since a flip-flop can only hold two values, such a device is said to hold a binary digit or **bit**.

Although, like neurons, there are many different types of flip-flops, we will consider only one type here. Our flip-flop has one information input wire, one information output wire, and one control wire. See Figure 2.1a. When the control input is off, the state of the flip-flop remains unchanged, either set or reset, regardless of the value of the information input. The information output is on when the flip-flop is set, and off when it is reset. When the control input, called the **copy input**, is turned on, the flip-flop prepares to change state. The flip-flop does not change state, however, until the very instant the copy input turns off. At that instant, the flip-flop is set if the information input is on or reset if the information input is off. Thus the state of the flip-flop is determined by the input information (on sets it and off resets it) at the time specified by the control input. The output of the flip-flop subsequently reflects its new state. The

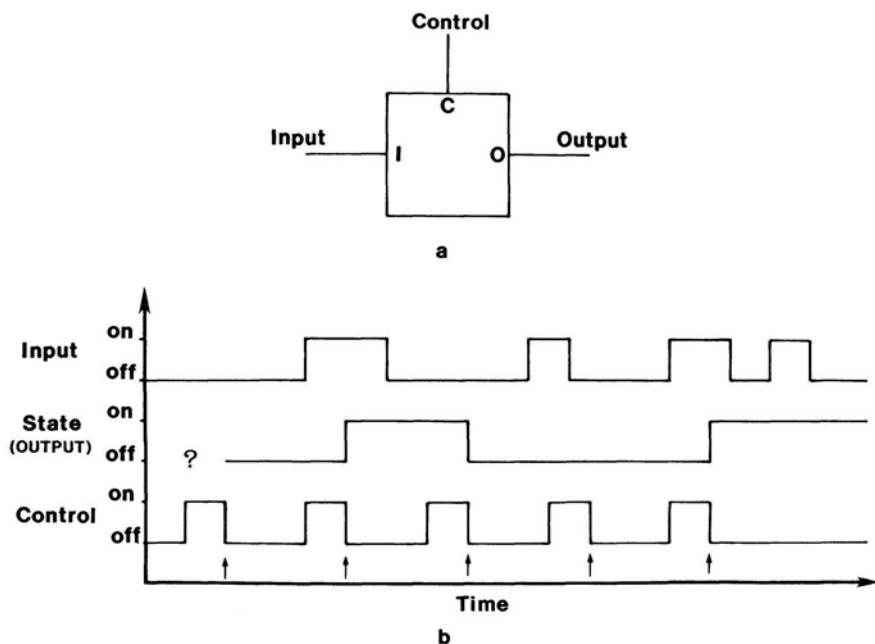


Figure 2.1. a) A flip-flop. b) A timing diagram showing the relationships between information inputs, control (or clock) inputs, and the state (hence output) of the flip-flop. For this flip-flop, a state change only occurs when the control input turns off (indicated by arrows). The new state is determined by the state of the input (on or off) at that instant. The question mark indicates that the initial state of the flip-flop is not known.

flip-flop then stays set or reset until the control input initiates another state change.

Flip-flops are generally grouped together into word-sized units which are controlled as a single device called a **register**. A register is a storage device that holds one word of information. See Figure 2.2. A four-bit register, for example, consists of four flip-flops and can therefore hold one four-bit word or one of 2^4 or 16 different patterns. An eight-bit register can hold one eight-bit word or one of 2^8 or 256 patterns. These patterns may represent numbers, characters, computer instructions, or some other set of logical quantities. The **copy input** to a register causes it to hold the value on the input lines just as the copy input to a single flip-flop caused that flip-flop to hold the last value on its input line. Table 2.1 shows several different four-bit information codes used today.

Registers are fundamental building blocks in computers. They are physically connected to other registers and other computer components (storage devices, processing units, and so forth) through data buses as described earlier. However, registers are not directly connected to data buses. They are connected to the

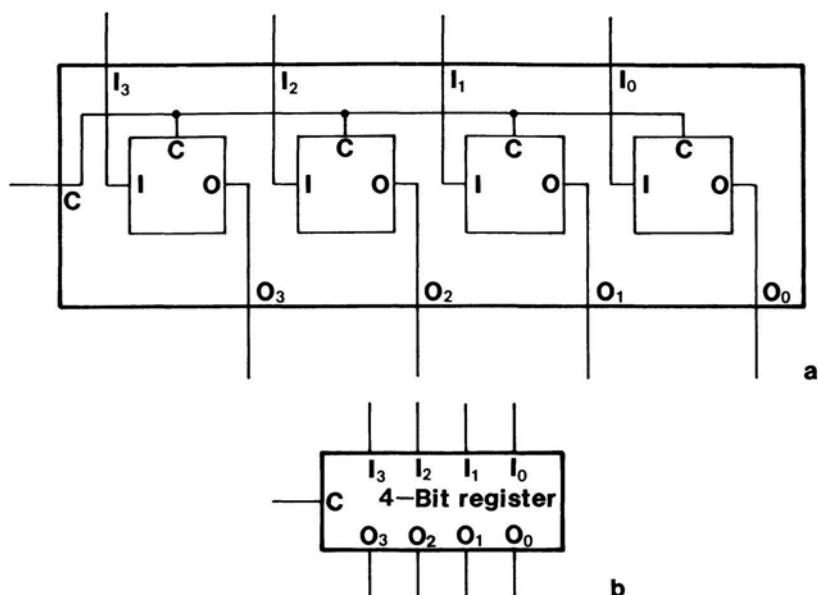


Figure 2.2. a) The circuit diagram for a 4-bit register composed of four flip-flops. b) The symbolic diagram of a 4-bit register.

TABLE 2.1
Common Four-bit Number Representations

<i>Absolute Binary</i>	<i>Decimal</i>	<i>Sign Magnitude</i>	<i>One's Complement</i>	<i>Two's Complement</i>	<i>Excess 3</i>	<i>Binary Fraction</i>
0000	0	0	0	0	-0	0
0001	1	1	1	1	-2	1/16
0010	2	2	2	2	-1	2/16
0011	3	3	3	3	0	3/16
0100	4	4	4	4	1	4/16
0101	5	5	5	5	2	5/16
0110	6	6	6	6	3	6/16
0111	7	7	7	7	4	7/16
0000	8	-0	-7	-8	5	8/16
1001	9	-1	-6	-7	6	9/16
1010	10	-2	-5	-6	7	10/16
1011	11	-3	-4	-5	8	11/16
1100	12	-4	-3	-4	9	12/16
1101	13	-5	-2	-3	10	13/16
1110	14	-6	-1	-2	11	14/16
1111	15	-7	-0	-1	12	15/16

buses through sets of switches, one switch for each bit in the register. This is illustrated in Figure 2.3. If the word size of a computer is four bits, then each register consists of four flip-flops and there are four switches that connect the four flip-flops of the register to the corresponding four wires in the data bus. The set of switches connecting a register to a data bus is called a **bus gate**, and in general the switches in a bus gate are all controlled by a single control signal which originates in the control unit of the computer. (Note that the control signal is such precisely because it is used as a control signal by the register.)

When the control signal opens the switches in a bus gate, the static pattern encoded by the register's flip-flops is impressed on the data bus. It is by this process that the static pattern in the register is converted into a dynamic pattern in the data bus that can be sensed by other components in the computer. Since the control unit generates the control signal that places data on the bus, it can at the same time signal other computer components to inspect the data bus and copy the information. It is by this very simple technique that information is transferred from one device to another during a computer's computations.

The brain is very different and vastly more complex than a digital computer. In the first place, neurons, which are the circuit components of the brain, are not simply on or off like flip-flops and wires. The information encoded in a collection of neurons is not represented by the states of the neurons at a particular time but by their rates of firing. Second, although information is conveyed from one part of the brain to another by the neurons themselves, the connections are not like the wires of a data bus that do not modify the signals they convey. Neurons *are* the computational elements of the brain, and computations often take place during information transfer. Finally, the number of neurons that encode patterns of information is significantly larger and the patterns themselves are markedly more complex than the patterns in a computer. The optic nerve, for example, which conveys the visual pattern from eye to brain, consists of more than a million elements; in a computer, a word size of 64 bits is considered very large!

NEURAL INFORMATION PATTERNS

Within a computer, the smallest indivisible unit of information is the bit, but the fundamental unit of dynamic information—the word—is the pattern of on-and-off signals in the wires of a data bus. Within the brain, the smallest indivisible unit of information is the rate of firing of an individual neuron but the fundamental unit of dynamic information is the **depolarization pattern**, the set of firing rates of the neurons in a specific collection of neurons.

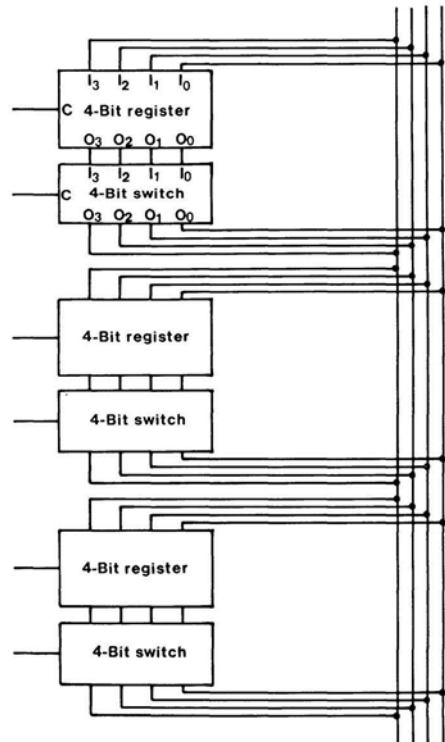
The data buses of the brain are the **neural pathways** or **nerves**. Neural pathways are collections of myelinated axons of particular sets of cells. The information being transmitted by a particular neural pathway is the pattern

generated by the neurons whose axons form the pathway. The transmitted pattern is the depolarization pattern sensed by the postsynaptic cells upon which the pathway terminates. The optic nerve is one example. It is comprised predominantly of the axons of retinal ganglion cells. The retinal ganglion cells perform the final stage of processing by the retina, so the optic nerve conveys the eye's representation of the ocular image to the brain. See Figure 2.4.

When describing neural information, one must always have in mind a specific collection of neurons, and the information pattern is specified by giving the rate of firing of each neuron in the collection, *not* by giving the state of each neuron at a particular time. For example, some of the axons in the optic nerve convey information from the brain to the eye. These efferent axons are not included in the pattern that describes the retinal output even though their activity may control the retinal output.

The **size** or **dimensionality** of a neural pattern is the number of axons conveying the pattern. Since there are approximately a million afferent axons (conducting information toward the brain) in the optic nerve, the afferent pattern conveyed by the optic nerve has size 1,000,000. In contrast, if it requires only three neurons to encode the color projected at a particular point on the retina, then the dimension of that subpattern is three.

Figure 2.3. Three 4-bit registers connected to a 4-bit data bus using three 4-bit switches to regulate the connections. When the "C" input to a 4-bit switch is on, each input is connected to its output (I1 to O1, I2 to O2, etc. as labeled in the upper switch only), and hence all outputs of the register are connected to the data bus. When the "C" input is off, the register is disconnected from the data bus. Note that inputs to the registers are connected directly from the data bus. This is okay since a register does not change state except when its "C" input is turned off. Said another way, the register ignores its input unless it is clocked.



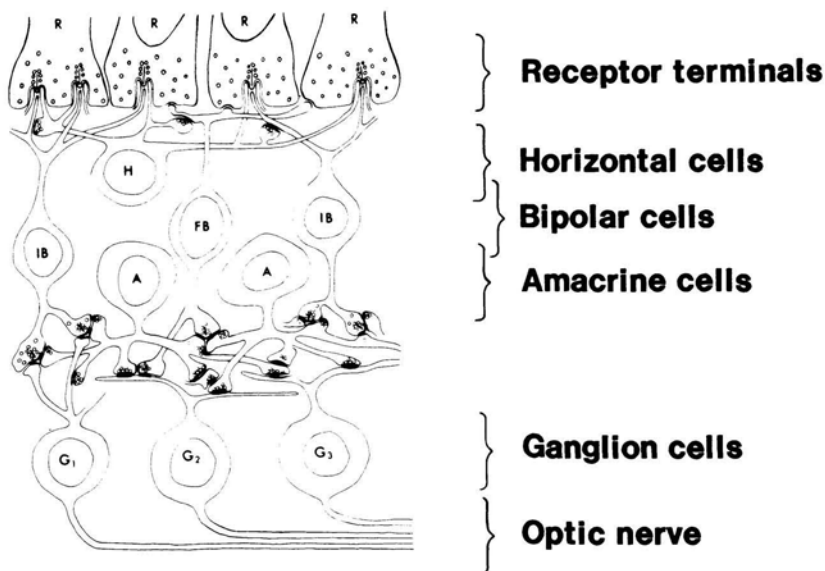


Figure 2.4. The synaptic structure of the retina showing that axons of the ganglion cells form the final pathway of visual information. Note the specialized synaptic structures. Compare this figure with Figures 7.6 and 7.7. (Reproduced, with permission, from J. E. Dowling, *Organization of Vertebrate Retinas*. *Investigative Ophthalmology*, 9, 1970, 655-679.)

Neural information patterns in general are **spatial, time-varying patterns**. They vary both as a function of the particular neuron in the collection and as a function of time. Many information patterns are two-dimensional, where the two dimensions represent the geometric coordinates of the incoming sensory signals (e.g., position on the surface of the skin, position on the retina of the eye), or the geometric coordinates of the origin of the pattern within the brain (e.g., position on the cerebral cortex).

As stated earlier, the firing pattern in a collection of cells varies as a function of time. I will use the notation $S(N)(t)$ to designate the rate of firing of cell N in collection S at time t , and I will use $S(t)$ to designate the firing pattern in the entire collection at time t . If the retinal ganglion cells are named RG , for example, then $RG(t)$ designates the afferent information conveyed by the optic nerve to the brain at time t and $RG(3,6)(t)$ designates the rate of firing of retinal ganglion cell $RG(3,6)$ at time t . A similar notation was used in Chapter 1 to represent the frequency of a mathematical neuron.

This notion of neural information is based on the fundamental assumption that neural interactions are statistical and neural information is encoded in terms of the firing rates of cells. Pulse height and relative phases between spikes are assumed not to be of primary concern. However, for those brain systems

where phase of depolarization is a critical parameter (for example, in the auditory system), this notion will need to be refined appropriately.

Describing Patterns in Neural Networks

The following descriptive mechanism is often convenient for describing the information in a particular collection of neurons. Imagine that each neuron in the collection can be connected to a small light bulb which glows with an intensity proportional to the rate of firing of the neuron. The light bulbs are then arranged in a geometric pattern determined by the intrinsic coordinates of the neurons in the collection. For example, light bulbs connected to retinal ganglion cells would be arranged in a pattern similar to the arrangement of the retinal ganglion cells themselves. An observer can now look at the light pattern just as he or she might look at a television screen and describe the neural activity as he or she would the picture on the screen. For example, he or she can describe the shape, size, position, and intensity of the activity within the collection.

Equality and Similarity of Information Patterns

The notion of equality of neural information patterns is fundamental and will be defined here. Two spatial neural patterns are **equal** in case two conditions hold: (1) There is a one-to-one correspondence between the cells in the two pathways that convey the patterns, and (2) The firing rates of each pair of cells under this correspondence are the same. Using the descriptive mechanism of the previous section, two patterns are equal if they look identical. Two spatial neural patterns are **similar** or **proportional** in case: (1) There is a one-to-one correspondence between the cells in the two collections, and (2) The ratios of the firing rates of each pair of cells under this correspondence is the same. For example, the firing patterns in two collections of cells are similar if the cells in the two collections correspond and the firing rate of each cell in the second collection is twice the firing rate of the corresponding cell in the first collection. Once again, using the descriptive mechanism of the previous section, two patterns are similar if they look the same only one is brighter than the other.

It is important to recognize that, according to this definition, two spatial neural patterns can be equal even if the corresponding neurons do not fire at corresponding times. It is only necessary that the **rates of firing** at corresponding times be equal.

I will now extend the notion of equality to spatial, time varying or **spatio-temporal** neural patterns. Two spatio-temporal neural patterns are **equal for T seconds** provided three conditions hold: (1) there is a one-to-one correspondence between the cells in the two pathways that convey the patterns, (2) there is a temporal correspondence between the onsets of the two depolarization patterns, and (3) the spatial neural patterns are equal at

corresponding times. This can be stated mathematically as follows. If I and O are the pathways, cell $I(M)$ corresponds to cell $O(M)$, and t_1 and t_2 are the onset times of the two patterns, then $O(M)(t_1 + t) = I(M)(t_2 + t)$ for all t between 0 and T . Thus two spatio-temporal neural patterns are equal provided there is a spatial and temporal correspondence between the patterns.

Two spatio-temporal neural patterns are **similar** provided that (1) there is a one-to-one correspondence between the cells in the pathways that convey the patterns, (2) there is a temporal correspondence between the onset times of the two patterns, and (3) the spatial patterns are similar at similar times after pattern onset. Again, this can be stated mathematically as follows. Using our earlier notation, the patterns $O(t_2)$ and $I(t_1)$ are similar in case $O(M)(t_1 + c_1 \times t) = I(M)(t_2 + t)$ for all t between 0 and T . Thus two spatio-temporal patterns are similar in case there is a spatial correspondence between them and one pattern either progresses faster or slower (or the same speed) than the other.

As an example, sentences read by the same person at different rates of speed are similar as are the images in a movie when played at normal speed or in slow motion.

Logical Categories of Patterns

Information input and output neurons were defined in Chapter 1 as were control and effector neurons. The patterns of information conveyed by these types of neurons are **input patterns**, **output patterns**, **control patterns**, and **effector patterns**. These are logical categories and depend not on the encoding of information in the pathways but on how the information is used.

SOME NEURAL NETWORKS

Having now built up a vocabulary for understanding the logical interactions between neurons, the final sections of this chapter will present several very simple neural network models for information transfer.

Transmission Lines

An **information pathway** consists of the set of myelinated axons of cells that transfer information from a **source** to a **destination**. The cells at the source whose axons form the pathway are **input cells**. They generate the **input pattern** that enters the pathway. The cells whose axons leave the pathway are **output cells**. They convey the **output pattern** from the pathway. The one requirement imposed on a pathway is that the input pattern equals the output pattern: The pathway must not modify the information.

The simplest realization of a pathway is when the input cells *are* the output cells so the pathway consists entirely of the axons of the input cells. In this case, the pathway is part of the source network. An alternate realization is that each input cell is either an output cell, or it connects to a single **intermediate** or **relay** cell. Each intermediate cell is either an output cell or it connects to another intermediate cell. Any number of intermediate cells may connect each input cell with one output cell, the connections all being sequential. When an input cell fires, the cell that it contacts fires, and so on until the output cell fires. Thus the output from a pathway is identical to the input except for a possible time delay in the pattern.

In the brain the most obvious candidates for pathways are the optic and auditory nerves. If, as in the auditory nerves, information is encoded in terms of the relative phases of depolarization between the cells, then the pathway must preserve the phase relationships or information would be lost or destroyed.

Switching Networks

A **switching network** is a network that has one or more collections of information input cells, one or more collections of information output cells, and one or more control inputs. The control inputs determine which information input cells will be connected to which information output cells. Three examples of switching networks and their graphic symbols are shown in Figures 2.5 through 2.7. The network in Figure 2.5 has one collection I of information input cells, two collections A and B of information output cells, and two control cells, C_1 and C_2 , which have inhibitive regulatory coupling. When control cell C_2 fires, the coupling between the information input cells and the information output cells will be inhibited where shown. This means that the input cells are only connected to the output cells of collection A. Connections to the output cells in collection B are blocked. Similarly, when control cell C_1 fires, the connections to the output cells of collection A are blocked, and the inputs are connected to the outputs named B. If neither control cell fires, then both collections A and B will receive copies of the input pattern, and if both control cells fire, no information will be transmitted.

The network shown in Figure 2.6 has two collections I and J of input cells and one collection K of output cells. Both input sets I and J stimulate the output cells, which fire at the sum of rates of the corresponding input cells. However, if only one of the input sets I or J is active, then the output pattern is equal to that input pattern.

A third example of a switching network is a shift network. Figure 2.7 shows a shift network having one collection R of input cells, one collection S of output cells, and five control cells C_1 through C_5 . When all five control cells fire, no information is transmitted from R to S. When control cell C_1 stops firing, the inputs are gated to output cells S_1 , S_2 , S_3 , S_4 , and S_5 , respectively. When control

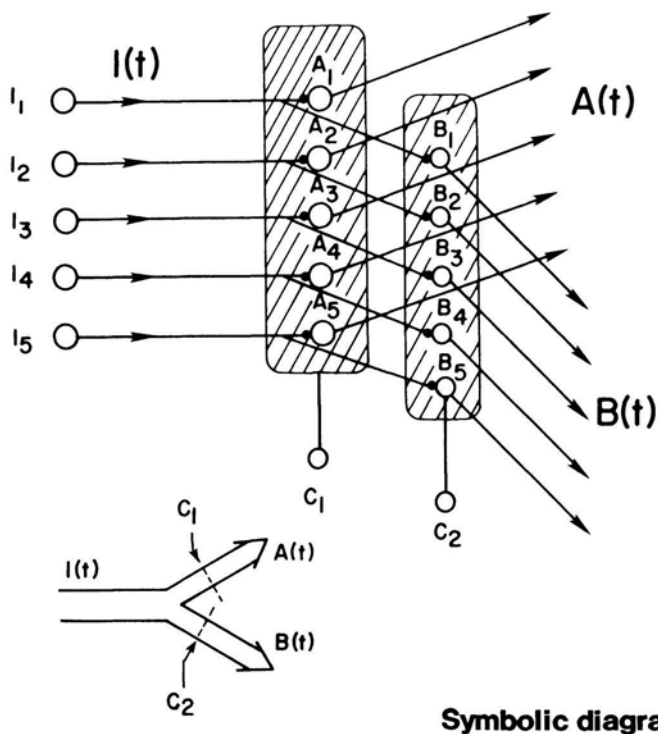


Figure 2.5. One way to use negative regulatory coupling to control information transmission along two pathways.

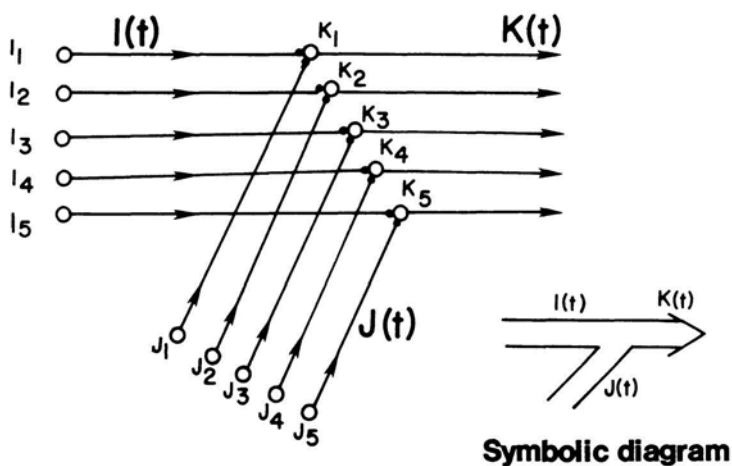


Figure 2.6. The uncontrolled merging of two information pathways.

cell C_2 stops firing, the inputs are gated to output cells S_2 , S_3 , S_4 , S_5 , and S_6 . When control input cell C_5 stops firing, the inputs are gated to output cells S_5 , S_6 , S_7 , S_8 , and S_9 . The network shifts the input pattern in the output cells as determined by the control pattern C .

Masking Networks

The notion of switching can be generalized so that the information in one or more of the information input cells is *selectively* allowed to pass to the corresponding information output cell. Consider the network shown in Figure 2.8. Each information input cell is connected to a single information output cell, and each connection is regulated by a different inhibitive control cell. If a control cell fires, then information will be blocked between the corresponding information input and output cells. If a control cell does not fire, then information will be allowed to pass. By presenting a spatial pattern to the control cells, the corresponding pattern will be blocked by the network; it will be **masked**. Figure 2.9 shows the appearance of an input pattern, a control pattern or **mask** and the corresponding output pattern for the network. A graphic symbol for a masking network is also illustrated.

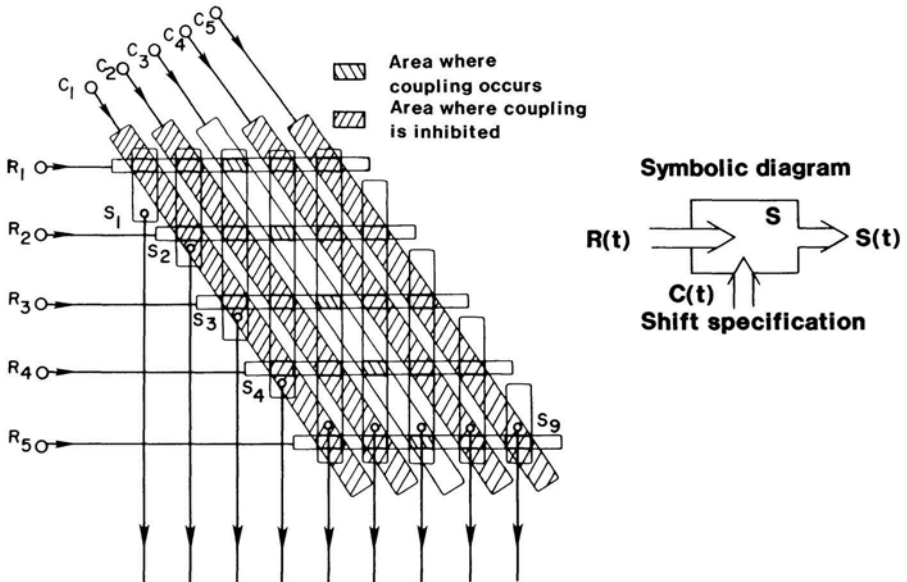


Figure 2.7. A shift network. Cells labeled R_1 thru R_5 convey the input pattern, cells labeled S_1 thru S_5 convey the shifted output pattern, and cells labeled C_1 thru C_5 control the amount of shift. The inset shows the symbolic notation for a shift network.