
ENCYCLOPEDIA OF COMPUTER SCIENCE AND TECHNOLOGY

EXECUTIVE EDITORS

VOLUME 4

Br to Chem

ENCYCLOPEDIA OF COMPUTER SCIENCE AND TECHNOLOGY

EXECUTIVE EDITORS

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VOLUME 4
Br to Chem

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BRAIN MODELS

VIEWS OF THE BRAIN

Early History [42, 54]

Up to this day we know less about the way our brain works than about the functioning of other organs in our body. But this has not inhibited numerous attempts at modeling throughout the ages, which have sometimes been interesting and sometimes amusing. Brain models have been created on the basis of discoveries in anatomy, physiology, and behavior, on the basis of natural or man-made analogs, and on the basis of what one may call inner experience.

The following is an example of an active versus a passive view of perception based, perhaps, on some differing aspects of inner experience. In the times of the ancient Greeks and even during the period when the Arab civilization flourished, but before light, optics, and visual anatomy and physiology were properly understood, there were opposing views of the visual process. According to one, "rays" emanated from the eyes to perceive the objects in the external world, while according to another, such "rays" entered the eyes from outside to carry the perception to the observer. Even today the active and passive aspects of perception are subjects of debate among philosophers and psychologists.

The Greeks believed in an essence of man, or "soul," which could embrace intellect and sensation. Philosophers like Philolaos (ca. 400 B.C.) and Aristotle (384-322 B.C.) regarded the heart rather than the brain as the supreme center of the "soul," since the brain cannot "feel." According to Aristotle, the brain was accessory to the heart. But Alcmaeon (sixth century B.C.), who is said to have been the first to dissect human bodies, knew that the brain was involved in sensation, movement, and thought, and he believed the brain to be the seat of the "ruling soul."

As usual, the physicians and dissectionists related their views on function more closely to the structures they observed. Hippocrates (fifth to fourth centuries B.C.) considered the cause of epilepsy to be located in the brain. Galen's views (second century A.D.) are of some interest for their detail and because they exerted a continuing influence through the Dark Ages and after. Based on his knowledge of body fluids and particularly on the cerebrospinal fluid that flows through the ventricles in the brain, Galen believed that man was permeated with a "vital spirit" originating in the liver and pumped to the brain by the heart. In the brain the "vital spirit" was refined into an "animal spirit" and from there it was pumped throughout the body by the ventricles. A "visual spirit" was pumped to the eyes, where it met the outer light and then flowed back to the brain to complete the visual act. Vision was the most important sensory modality and the eyes were placed optimally for sight. Thus the brain, which was the seat of the reasoning soul, was placed close to the

eyes, and it followed that the other sense organs like ears and nose had to be in the head. Galen distinguished three primary functions of the brain: perception, thought, and memory. Some thirteen centuries later Leonardo da Vinci, whose own knowledge of anatomy was extensive, nevertheless wrongly sketched the brain with three bulbous spaces, one after the other, where perception, thought, and memory were localized. Thus was the longevity of Galen's ideas!

Beginnings of Present-Day Anatomy and Physiology [42, 54]

Ancient science and medieval superstition began to give way when Vesalius founded a systematic, scientific anatomy in the sixteenth century. But advance was slow. The beginnings of modern physiology hardly got under way until the eighteenth century with Haller (1708–1777), Gall (1758–1828), and later Flourens (1794–1867). There developed a controversy which is still with us today. One school held that different functions were localized in different parts of the brain; the other school maintained that the brain is "equipotential," that it acts as a single, integrated organ. Gall was an enthusiastic proponent of localization. "Psychic" functions like instinct of procreation, religiosity, and avarice were assigned by Gall to various cerebral loci. The pseudoscience of phrenology later based itself on Gall's teachings. On the other hand, Haller and Flourens, from their experimental and clinical observations, concluded that in spite of some localization the brain was an equipotential organ. Flourens found that cerebral ablations seemed to produce disturbances in proportion to the mass extirpated. However, the observational and experimental techniques of the time were rather crude and the conclusions cannot be upheld on the basis of more refined tests.

Major advances were made in the nineteenth century through the discovery of various brain centers which were involved in specific functions. As examples, one may mention Broca's speech area named after the discoverer, Fritsch and Hitzig's discovery of a somatomotor area, and Munk's discovery of the visual cortex.

The Greek's quest for the "ruling soul" was pursued in different ways. Thus in the seventeenth century Descartes proposed that the pineal body was the seat of the essence of mind. According to Descartes, such a locus would have to occupy a central position in the brain, and this made the pineal body an ideal candidate.

Psychophysiology and Neural Machinery

In the late nineteenth and our own twentieth century the pace of progress has greatly accelerated. Hughlings Jackson, (1835–1911) came to the conclusion that epileptic fits arise in local foci in the brain as a sudden and excessive discharge of nerve cells. He was much concerned with the multiple representation of function at different levels of the nervous system; namely, at the

elementary spinal level, at an intermediate motorsensory level in the brain, and at the highest level of the frontal cortex. Somewhat later, Penfield and his collaborators carried out extensive investigations during the course of their neurosurgical work on epileptics. They identified numerous areas of the cerebral cortex associated with various functions: motor, sensory, speech, auditory, and visual memory. A well-known example of their work, illustrated in Fig. 1, is the finding that the whole body surface and body parts are mapped onto the "somatosensory" cortex and the primary "motor" cortex, respectively. This was also the time of Pavlov's (1849–1936) famous behavioral experiments on conditioned reflexes [50]. Pavlov's approach has become dominant in Russia where attempts are made to reduce all brain activity to a superposition of reflex mechanisms [42, 61]. Sherrington (1857–1952) was interested in the integrative action of the nervous system [64]. He examined a number of phenomena in great detail including the reciprocal activity of agonist and antagonist muscle groups, sensory facilitation between distant body parts, and central inhibition. He postulated that neural interactions were mediated through physical-chemical changes at the junctions between nerve cells, which he called "synapses." The existence of separate nerve cells was not, however, universally accepted. Some thought that the whole nervous system consisted of

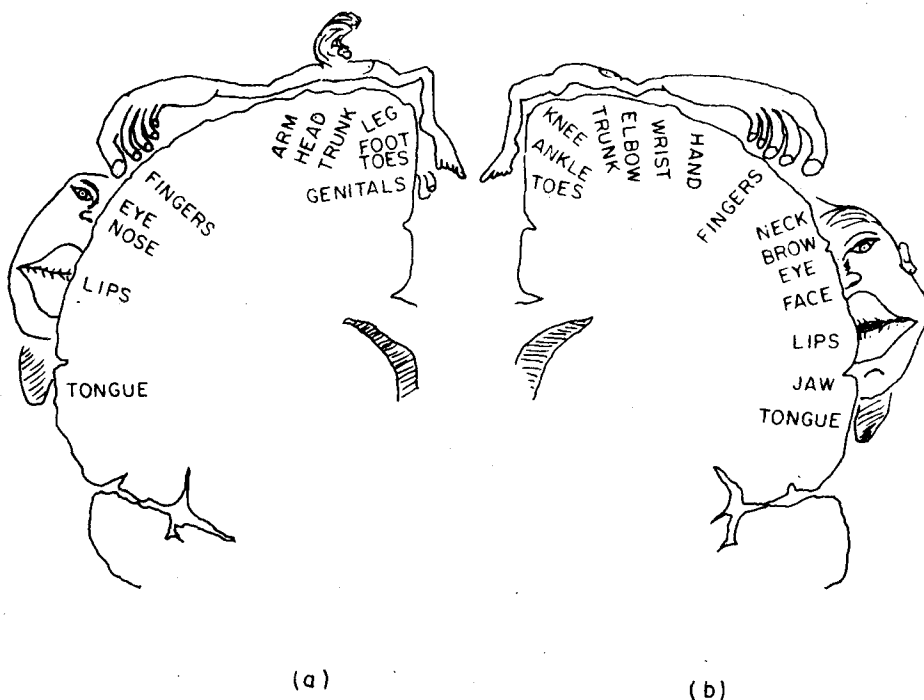


Fig. 1. Somatotopic projections: (a) primary sensory cortex; (b) motorsensory cortex. Sizes of body parts and lengths of bars indicate extent and location of cortical areas whose stimulation evoked responses in the corresponding body parts [51].

BRAIN MODELS

a continuous netlike web. It was not until Ramon y Cajal (1852–1934) showed by his remarkable and detailed microscopic investigations that there were indeed separate cellular entities that the neuron came to be universally regarded as the basic cellular unit of the nervous system [8].

Through the work of Pavlov, Sherrington, Cajal, and others there began to emerge the relationships between structure and function, between behavior and neural machinery. Further investigations of these relationships have continued to this day, where one may mention among many examples in more recent times the work of J. Z. Young and his group on the behavior, anatomy, and physiology of octopus [71]; numerous studies on arthropods such as the work of W. Reichardt's group oriented toward systems analysis [70]; and the work on the neuronal "machinery" of the cerebellum by Eccles, Ito, and Szentágothay [19].

Wherever the seat of the "soul" may be, present scientific investigations of brain structure and function with their associated behavioral manifestations are restricted to those aspects which can be described in terms of physical and chemical parameters.

NEURON MODELS

Models of the brain must necessarily embrace models of neurons and neural activity. We know that neurons, like most cells, maintain a negative electric potential inside the cell with respect to the outside, and that unlike other cells, neurons respond to stimulation with changes of potential. It was Galvani who discovered "animal electricity" toward the end of the eighteenth century, and Nernst (1864–1941) showed that differences of ionic concentration on two sides of a semipermeable membrane were accompanied by differences of potential. In the 1920s Adrian and others began investigations on the transmission of waves of electric potential in nerve trunks. It was realized that neurons can transmit changes of potential in the form of "impulses," and that the generation and transmission of these impulses was related to ionic exchanges across the cell membrane. The detailed mechanisms were described by Hodgkin and Huxley in 1952 [27].

Neurons are distinguished from other cells not only by their electrical activity but also by their shape. Long fibers project from the cell body and conduct the electric signals from and to other neurons. The output signals of a neuron usually consist of one or more brief voltage pulses which travel with constant amplitude and constant speed along the "axon," one of the fibers projecting from the cell body. When this signal reaches a "synapse" it is transmitted to an adjoining neuron, generally through a chemical mediator. In addition to the axon, a neuron has a number of other fibers projecting from the cell body. These are the "dendrites," which may be considered as the input lines. Synapses are found mostly on dendrites, but also on the cell body and axon. Unlike the axonal signal, the signals transmitted by the dendrites usually decay in amplitude as they are propagated along the fiber, rather like an

electric disturbance in a leaky cable. The synaptic inputs may be excitatory or inhibitory. They are summated and conducted by the dendrites toward the cell body. When a certain excitatory threshold level is exceeded, an "action potential" is set off. This is the brief voltage pulse which travels down the axon. The cell thus balances excitation against inhibition, and the output is determined by this balance as well as by the internal state of the cell.

The negative internal potential in the resting state of the cell is maintained primarily by differences of concentration of sodium and potassium ions on the two sides of the cell membrane. In the resting state the cell is relatively permeable to potassium but relatively impermeable to sodium which is constantly pumped out of the cell as fast as it leaks in. Changes of potential and departures from the resting state can be brought about by selective changes in the ionic permeabilities of the membrane, which lead to an exchange of ions across the cell membrane. Thus the interior of the cell can be depolarized (i.e., it becomes less negative with respect to the outside) or hyperpolarized (more negative with respect to the outside), depending on the prevailing ionic concentrations and depending on which ions are made to flow across the membrane. The action potential is a depolarization which is set off by an initial, depolarizing membrane potential above the threshold for excitation. It is this initial potential which triggers a change of permeability, first for sodium and then for potassium. On the other hand, at "synapses" where transmission of the signal is most frequently mediated by chemical transmitters, the latter may alter the membrane permeabilities in a variety of ways, depending on the transmitter and on the properties of the target membrane. As a result, the adjoining membrane can be either depolarized or hyperpolarized [17, 31], depending on whether the synapse is excitatory or inhibitory, respectively.

The Hill-Rashevsky Model

In the 1930s, when the mechanisms for generating and transmitting neural signals were not as well understood as they are today, A. V. Hill and N. Rashevsky independently proposed equivalent models which contained two parameters, one excitatory or activating, the other inhibitory or inactivating [25, 57]. The balance of activation and inactivation could mimic the changes of potential which had been observed in nerve as a result of stimulation. Rashevsky's model is contained in the pair of equations:

$$d\epsilon/dt = KI - k(\epsilon - \epsilon_0)$$

$$dj/dt = MI - m(j - j_0)$$

ϵ and j are the excitatory and inhibitory parameters, respectively, I is a current stimulus applied to the nerve, and K, k, M, m, ϵ_0 , and j_0 are constants. Various experimental findings could be simulated with the aid of these equations. For example, it was known that a certain threshold quantity of steady current has to be delivered in order to produce excitation. The stronger the current, the

shorter is the required time of application, but the relationship between time and current is nonlinear. The Rashevsky-Hill equations can be fitted to these data, as they can also be fitted to subthreshold responses of nerve. In addition, Rashevsky attempted an analysis of nerve conduction, but the data available to him were too meager for any reliable conclusions. The Rashevsky-Hill model has been superseded by the much more powerful and precise model of Hodgkin and Huxley.

The McCulloch-Pitts Model

A model which has exerted considerable influence in theoretical studies is due to McCulloch and Pitts [43]. Since a neuron has a number of fibers some of which, the dendrites, can be considered as input lines and others, the axon, can be considered as the output line, and since a certain excitatory threshold has to be exceeded before an output is produced, McCulloch and Pitts modeled the neuron as a threshold element. This is shown in Fig. 2. There are a number of excitatory and inhibitory input lines and one output line. Any line can be either active or inactive. When the excitation exceeds inhibition by the threshold quantity h , an output is produced. The McCulloch-Pitts model is a digital model. That is, activity is in the form of a pulse and time is quantized in discrete intervals. In each interval the sum of the excitatory and inhibitory inputs is formed and the output is produced after a delay of one time interval. The activity on an excitatory line may be represented by $+1$ and on an inhibitory line by -1 . Inactivity is represented by 0. It can be shown that threshold elements of this type can perform logical operations. This is illustrated for conjunction, disjunction, and negation in Fig. 3. Thus a logical calculus can be used to analyze networks of such elements. A simple network is shown in Fig. 4. It corresponds to the proposition $\alpha \wedge \bar{\beta} \vee \bar{\alpha} \wedge \beta$. Its interest with regard to neural modeling is that it represents a contrast detector. For, as can easily be shown, an output will occur if and only if α or β , but not both, receive a stimulus. Thus it might represent a network for responding "visually" to a light-dark boundary, or by "touch" to the edge of a solid object, or through some other sensory process to the presence of a contrast.

Numerous other examples could be cited. Suffice it to mention that von Neumann [68] used the McCulloch-Pitts model in a classic analysis of

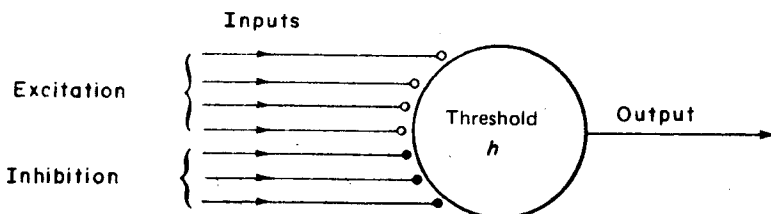


Fig. 2. A threshold element models the McCulloch-Pitts "neuron" [34].

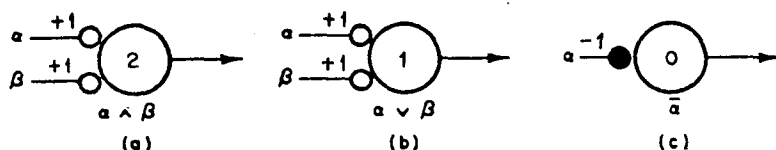


Fig. 3. McCulloch-Pitts "neurons" performing basic logic operations [34].

"probabilistic logic" in relation to automata theory. He showed how reliability of operation could be attained through randomization of input lines in a "restoring unit" and through the duplication or "multiplexing" of lines. His results are of interest to brain theory for they demonstrate, among other things, a possible functional significance for a random connectivity.

Stochastic Models

Like any biological unit, a neuron does not operate with unfailing regularity like a digital clock. The internal state of a neuron is subject to some variability which affects the output and hence also the input to other neurons. In addition, there may be transmission fluctuations both in the input and the output. Thus a statistical description of neural activity is called for. If it were possible to give such a description in sufficient detail, one might be able to separate the contributions of input and internal state to the fluctuations and shed further light on the generation and transmission of nerve impulses. Unfortunately this is not yet the case at present.

In modeling, one has to distinguish between a maintained discharge or

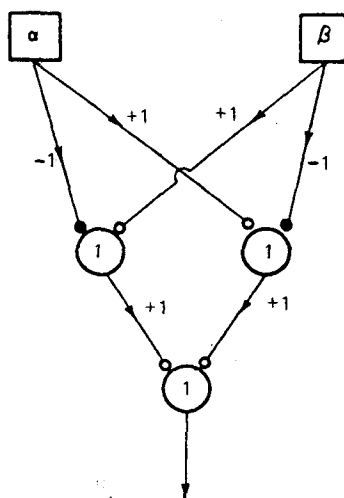


Fig. 4. A network of threshold units that performs contrast detection [34].

spontaneous activity on the one hand and activity due to stimulation on the other hand. It is usually found that the variability of neural discharges decreases upon stimulation. Maintained activity may be due to a variety of causes, such as a regular input source, or to internal "noise," or to the spontaneous presynaptic release of transmitter in the absence of stimulation. The occurrence of an input can sometimes be described on *a priori* grounds by a Poisson distribution or by a Gaussian distribution. For the Poisson distribution, the probability that n input events take place in time t is $(pt)^n \exp(-pt/n!)$, where p is the mean input rate and an "event" is the occurrence of a postsynaptic potential. Under suitable conditions, as the number of events increases, the discrete Poisson distribution tends to the continuous Gaussian distribution with probability density $\exp[-(x - m)^2/2\sigma^2]/\sqrt{2\pi}\sigma$, where x is the random variable, m is the mean, and σ is the standard deviation. Well-known examples of these two distributions occur at the neuromuscular end plate [5, 31]. This is a specialized junction between a motor neuron and a muscle fiber. When the action potential in the motor neuron reaches the end plate, a transmitter is released and initiates contraction of the muscle fiber. However, there is also a spontaneous release of transmitter in the absence of nerve impulses. It is found that the transmitter is released in certain sized "packets." The size of these packets, from the observations of spontaneous potentials, can be described by a Gaussian distribution, while the number of packets released by a nerve impulse can be described by a Poisson distribution.

Another example to which a stochastic treatment has been applied is the generation of nerve impulses taking into account excitation and inhibition, the variable delays between stimulus and response, and possible fluctuations in threshold. A simple model will illustrate how some of the variables enter the calculations. Suppose there are excitatory and inhibitory inputs which are transmitted along the dendrites to the axon hillock, the region on the axon where an action potential is initiated. Let ϵ and ι be the strengths of the excitatory and inhibitory signals, respectively, at the axon hillock. Let p_ϵ and p_ι be the probabilities of occurrence of excitation and inhibition, respectively. Due to the leaky properties of the neural membrane, excitation and inhibition both decay. Suppose the decay is exponential with a time constant τ . Then, starting from zero depolarization at time 0, the depolarization of the axon hillock at time t will be

$$\int_0^t (\epsilon p_\epsilon - \iota p_\iota) \exp[-(t - t_1)/\tau] dt_1 = (\epsilon p_\epsilon - \iota p_\iota) \tau [1 - \exp(-t/\tau)]$$

If a threshold depolarization h is required to initiate an action potential, it follows from the last equation that the expected firing time is

$$t_m = -\tau \ln [1 - h/\tau(\epsilon p_\epsilon - \iota p_\iota)]$$

More complex models have been investigated, which include internal noise and a resetting of the membrane potential to the resting level after each spike. When the excitatory and inhibitory inputs occur at random, one may use the

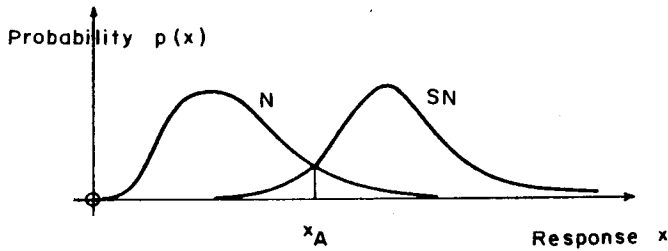


Fig. 5. Probability distributions for the depolarization of a neuron due to noise (N) and to signal and noise (SN). The threshold x_A is set so that the neuron fires when the (SN) probability is greater than the (N) probability [34].

analogy of a random walk with an absorbing barrier which is well known in the statistical literature. The "random walk" corresponds to the random occurrence and summation of synaptic inputs, and the "absorbing barrier" corresponds to the threshold at which the membrane potential is suddenly amplified and then reset to zero. As a continuous approximation, one may model the random walk process by analogy with diffusion. The probabilistic diffusion equation has been used extensively in the physical sciences and more recently also in modeling neuron firing statistics (for reviews see Refs. 22 and 48; see also Refs. 21 and 29).

As a consequence of the variability of neuronal activity and due to the presence of a threshold, a neuron can be viewed as a statistical decision element [34]. This is illustrated in Fig. 5 where the curve marked N for "noise" denotes the probability distribution for membrane depolarization in the absence of a stimulus; the curve marked SN denotes the probability distribution of membrane depolarization when a signal as well as "noise" is present. These depolarizations do not take into account impulse firing. But now x_A is set as a threshold level for firing. In the case of Fig. 5, the threshold would serve to distinguish signals from noise on the basis of a greater probability: to the right of x_A , SN has a greater probability than N and the cell would fire. Other criteria are possible, however, and would lead to different values for x_A .

The Work of Hodgkin and Huxley, Eccles and Katz

We recall that the action potential is propagated along the axon with constant speed and constant amplitude. At any point on the membrane the shape of the action potential as a function of time is illustrated in Fig. 6 on the curve marked ϕ . The ordinate is read from the scale marked mV and measures the potential above the resting level which is taken as zero. If this curve is turned left to right and slid along the x -axis at constant speed, it demonstrates how the potential wave propagates along the fiber. Since it is known that the nerve

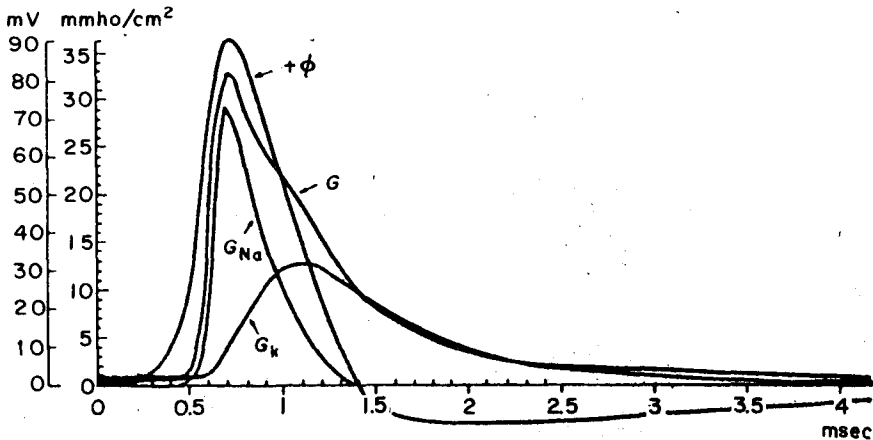


Fig. 6. Numerical solution of Hodgkin-Huxley equation showing components G_{Na} , G_K of membrane conductance G (in thousandths of reciprocal ohms per square centimeter) during propagated action potential ϕ [27].

membrane is permeable to various ions and electric current, one might expect a potential wave which disturbs the steady state to be attenuated as it propagates. This would be the case in most dendrites which act like leaky cables. The fact that the action potential is transmitted with constant amplitude suggests that there is a regenerative mechanism.

As mentioned earlier, the differences of potential across the membrane follow differences of ionic concentration and permeability. Hodgkin and Huxley showed that ionic exchanges are involved in the propagation of the action potential. The ions involved are primarily sodium and potassium, and in addition there are chloride and some other ions which leak passively through the membrane. In the resting state the ratios of sodium and potassium concentrations inside and outside a squid giant axon are about 1:10 and 30:1, respectively. Any sodium that leaks into the cell is actively pumped out and the membrane is relatively impermeable to sodium. But potassium can move across the membrane much more freely. The resting potential is thus close to the Nernst diffusion potential for potassium, which is about -77 mV in the squid giant axon. When the axonal membrane is depolarized by a certain subthreshold amount, say 5 mV, the depolarization propagates along the fiber and is attenuated in the process as in a leaky cable. But if the depolarization exceeds the threshold value, then instead it is suddenly amplified (for example to a pulse of some 90 or 100 mV in the squid giant axon) and then returns again to its original value as shown in Fig. 6. Working mostly on the squid giant axon, Hodgkin and Huxley [27] showed that the amplification of the potential and its subsequent return to the resting value were due to accompanying changes of the membrane conductances for sodium and potassium. These changes are shown on Fig. 6. G_{Na} is the time course of the sodium

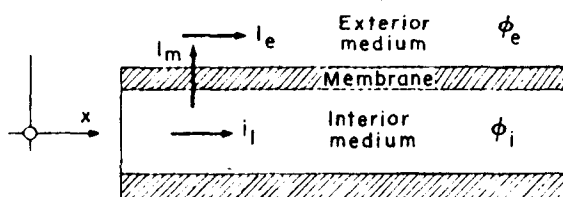


Fig. 7. Potentials and currents in a length of cylindrical fiber [34].

conductance, G_K that of potassium, and G is the net membrane conductance. When the threshold depolarization is reached, the sodium conductance increases rapidly and sodium ions rush into the cell, thus moving the membrane potential toward the sodium equilibrium potential, which is about 50 mV in the squid axon. Then the sodium conductance is inactivated and the potassium conductance begins to rise. The membrane potential moves back toward the potassium equilibrium potential and conductances and potential settle back to the original state.

The potentials and currents in a segment of membrane are illustrated in Fig. 7. ϕ_e and ϕ_i are the external and internal potentials, respectively, i_e and i_i are the external and internal currents, and i_m is the current flowing across the membrane. The membrane has a fairly constant capacitance, typically $1 \mu\text{F}/\text{cm}^2$. Hodgkin and Huxley modeled a membrane patch by the equivalent circuit shown in Fig. 8(a). C_m represents the membrane capacitance and there are

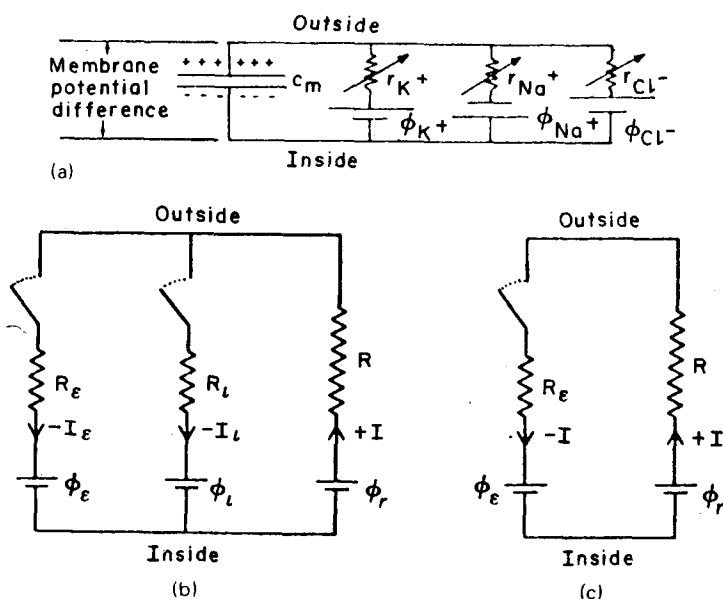


Fig. 8. (a): Membrane equivalent circuit [34]. (b) and (c): Simplified models of postsynaptic membrane [34].