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ON THE STRUCTURE AND ORGANIZATION OF THE NERVOUS SYSTEM FROM AN INFORMATION PROCESSING POINT OF VIEW

(NEURAL CODING, VISION, AND MOTOR CONTROL)

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THE OHIO STATE UNIVERSITY RESEARCH FOUNDATION

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FOREWORD

This study was initiated by the Biophysics Laboratory of the Aerospace Medical Research Laboratories, Aerospace Medical Division, by The Ohio State University Research Foundation of Columbus, Ohio, under Contract No. AF 33(657)-9660. Dr. N. A. Coulter, Jr., was the principal investigator. Lt. Col. Jack E. Steele, of the Mathematics and Analysis Branch, Biodynamics and Bionics Division, was the contract monitor for the Aerospace Medical Research Laboratories. The work was performed in support of Project 7233, "Biological Information Handling Systems and Their Functional Analogs," and Task 723304, "Neural Networks."

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The author acknowledges the invaluable assistance of Alfonso Angelone, Syed Fazal Mohammad, David E. Scott, and Jan C. West.

This technical report has been reviewed and is approved.

J. W. HEIM, PhD
Technical Director
Biophysics Laboratory

ABSTRACT

A study was made of the central nervous system from an information processing point of view. The study entailed a review and critical analysis of several hundred references, and involved a considerable amount of recasting and reorganization of existing knowledge into the terms and concepts of engineering, with particular reference to potential bionic applications. The study was selective rather than comprehensive. The neural coding problem was first examined, the history of efforts dealing with this problem was reviewed, and a mathematical representation of neural signals (neurograms) and neural operators was formulated. The processing of data by the visual system was then described, with particular reference to form, color, and movement detection, the temporal continuity of visual objects, image fixation, automatic focussing control, intensity control, image fusion, depth perception, and the stabilization of visual space. Next, the neural control of movement was analyzed from a servomechanical viewpoint. The unit biomechanical control system was defined, and the corticospinal command of this unit system was discussed. The cerebellar coordination and extrapyramidal stabilization of sequences and combinations of biomechanical control unit actions was examined. Finally, the ability of the central nervous system to generate its own goals--a capability for which no technological counterpart yet exists--was discussed, and a preliminary sketch of a theory of teleogenetic systems was presented.

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TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS (Continued)

I. THE PROBLEM OF CODING IN THE CENTRAL NERVOUS SYSTEM

INTRODUCTION

"In studying the nervous system or its elements and components as information handling devices, it is possible to abstract the informational characteristics entirely from the nature of the events which constitute the signals. Just as the nature of electricity or of magnetism is irrelevant to the patterns which constitute the characteristics of the messages transmitted over a telegraph wire, so are the physical aspects of the signals irrelevant to the study of the informational-handling characteristics of neural components." Rapoport and Horvath (1960).

What is meant by the term "information processing" when applied to the central nervous system?

In communication networks, the term "information" is precisely defined by the mathematical formulation of information theory. Given a collection of possible unit messages whose frequency distribution is known, if P_m is the probability of message m, the information transmitted by m is

$$H_m = -\log P_m \quad .$$

The information of the ensemble of messages is

$$H_t = -P_m \log P_m \quad .$$

It is, of course, possible to apply this definition to neural processes (Mackay and McCulloch, 1955; Rushton, 1961; Grusser, 1962; Barlow, 1963), but this should be done with caution. In the first place, as Shannon (1948) pointed out, the technical definition used in information theory is of value primarily in determining economy and efficiency of communication networks. Other mathematically defined concepts may be more suitable in describing neural signals. In the second place, this gives undue emphasis to one type of neural event -- the nerve impulse. A number of workers have recently pointed out, however, that other neural events may be of equal or even greater importance in central neural processes. Among these are the nonpropagated "electrical waves" that apparently form the basis of the electroencephalogram (Bishop, 1956; Grundfest, 1957; Purpura, 1959), and glia cell control of neuronal processes (Galambos, 1961; Svaetichin et al. 1961; Lipetz, 1963).

In most of the neurophysiological literature, the term "information" is used in a descriptive sense roughly equivalent to "signal." This usage will be followed here, unless otherwise specified. It is evident that what might be called the "neural coding problem" -- the matching of mathematically formulable properties of nerve impulse patterns to relevant physiological and psychological functions -- has not yet been solved.

A brief survey of efforts to deal with the neural coding problem may provide a useful perspective.

HISTORICAL SURVEY

The development of electrophysiological techniques and single fiber recording in the 1920's disclosed an empirical relationship between the intensity of a stimulus and frequency of nerve impulses. In the steady state, the frequency was found to be proportioned to the logarithm of stimulus intensity. This relationship has been shown to hold for a large variety of receptors. (Adrian, 1926; Matthews, 1931; Hartline and Graham, 1932; Bronk and Stella, 1932; Gray, 1959). Similarly, a relationship between frequency of impulses and force of contraction of skeletal muscles was demonstrated (Adrian and Bronk, 1928, 1929; Lindsley, 1935). As a result of these studies, it was natural to view the central nervous system as a communication network employing a form of pulse frequency modulation.

The first attempt to develop a mathematical theory of the central nervous system was made by Rashevsky (1938). This attempt was actually an extension of an earlier theory of peripheral excitation (Rashevsky, 1933, 1936; Hill, 1936; Monnier, 1934). Rashevsky postulated the existence of two quantities, an excitatory state ϵ and an inhibitory state j, governed by the differential equations

$$\frac{d\epsilon}{dt} = a(\phi-\epsilon) \qquad (1)$$

and

$$\frac{dj}{dt} = b(\psi-j) \quad , \qquad (2)$$

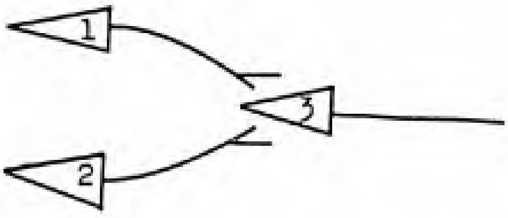
where ϕ and ψ are functions of the frequency, and $\underline{a}$ and $\underline{b}$ are constants.

Elaborate mathematical models of hypothetical neural networks were explored by Rashevsky and his colleagues (see Householder and Landahl, 1945).

In 1943, McCulloch and Pitts published a paper entitled "A Logical Calculus of the Ideas Immanent in Nervous Activity." In essence they applied Boolean algebra to the representation of the behavior of small neural networks. An example of a statement in this calculus is

$$N_3(t) \equiv N_1(t-1) \cdot N_2(t-1) \quad .$$

This represents a net pictured below.



The statement may be read as follows: Neuron N_3 fires at time t if and only if neuron N_1 fires at time (t-1) and neuron N_2 fires at time (t-1).

Here time is measured in units of "synaptic delays" (approximately one millisecond).

Landahl, McCulloch, and Pitts (1943) also showed that the propositional expressions of the McCulloch-Pitts calculus could be converted by a simple set of rules into probabilistic relations applying to large numbers of neurons and interconnections. This appears to have been the first "probabilistic" approach to neural networks. Since then emphasis on probabilistic approaches has grown (Shimbel and Rapoport, 1948; Cragg and Temperley, 1954; Von Neumann, 1958; Rosenblatt, 1962). The impact of information theory has undoubtedly played a major part in this trend.

Each of these approaches has abstracted one aspect of neural phenomena as a basis for formulating mathematical models whose implications were exploited. None should be accepted uncritically; rather, they should be regarded as useful pilot explorations. A definitive theory of neural information processing is a task for the future.

REPRESENTATION OF NEUROGRAMS

It is convenient to separate information processing in the central nervous system into two main categories.

1. The transmission of information by patterns of nerve impulses along axons.
2. The processing of information by neuroanatomical structures and neurophysiological mechanisms in presynaptic arborizations, transynaptic processes, dedrites, and cell bodies.

We refer to an impulse pattern as a neurogram, emphasizing by this term the informational aspect of neural processes. The action of neuroanatomical structures and neurophysiological mechanisms upon neurograms we call an operation. Just as a voltage wave form may be amplified, filtered, used to modulate a carrier, etc., in electrical circuits, so a neurogram may be subjected to a variety of neural operations in neural networks.

There is a variety of ways in which a neurogram may be represented mathematically. We shall consider the seven types of representation:

1. Binary
2. Frequency
3. Pulse Interval
4. Channel
5. Set Theoretic
6. Symbolic
7. Property Coded

The simplest representation is the binary type. At any given quantal moment, the impulse activity of a group of neurons (axons) can be represented by a collection of binary digits, 1 representing presence of an impulse, 0 no impulse. (Actually, it is necessary to specify a particular part of a neuron known to be capable of conducting impulses, since it is possible for a given axon to be excited by more than one impulse at a given time. For convenience, we will assume all neurograms refer to the impulse-initiating segment of a neuron, unless otherwise specified.) Thus, five neurons might transmit a neurogram (10110) at a given moment.

The time quantum of a binary neurogram will be assumed to be one millisecond, unless otherwise specified. This corresponds to the minimum absolute refractory period of most neurons (Davies, 1961).

Since impulse frequency appears significant in some ways (see above), another representation used is the frequency representation. Here we encounter a problem analogous to that expressed by the Uncertainty Principle of Quantum Mechanics -- it is impossible to define an instantaneously continuous frequency for a digital process. Many authors define frequency as the reciprocal of the pulse interval, and arbitrarily assign the time as halfway between the impulses. Others take an average frequency, counting impulses over an interval of time. The general problem of pulse-frequency representation has been discussed by Jones et al. (1961).

Since our interest is focussed on impulse patterns of groups of neurons, we shall use the average frequency over a specified time quantum -- say 10 milliseconds -- simply counting impulses present within the time quantum.

Another possible representation, the pulse-interval representation, is simply the reciprocal of the frequency. It may be of value in certain applications.

In at least some functions under control of the central nervous system, a group of neurons perform equivalent functions. For example, the alpha motoneurons innervating a given skeletal muscle all perform the same function -- evoking a contraction of the muscle. The tension or shortening developed by the muscle depends not on which motoneurons are previously fired, but on the number of motoneurons active. Hence, we can say that the alpha motoneurons innervating a particular skeletal muscle are functionally equivalent. Such a group of functionally equivalent neurons we call a channel.

It is evident that we can define channel frequency simply by counting impulses in the channel during a specified time quantum. This is the basis for the channel representation of neurograms.

Thus far, the various representations of neurograms considered make no distinction among the elements of the representation. However, many neural phenomena, such as local sign and topographic projection, indicate that order of position of a neuron or a channel is important. This leads to the set-theoretic representation.

The potential significance of the set-theoretic representation may be conveyed by the analogy that the set-theoretic representation is to the binary (or frequency) representation as pulse code modulation (PCM) is to pulse amplitude modulation (PAM) in telephonic networks. In pulse code modulation, the position of the pulse in a short train is used to transmit information according to a binary code. Thus an amplitude of 6 is represented by 110. In the set-theoretic representation the position of an element of the neurogram is considered to be informationally significant.

In what follows we shall, for convenience, use the binary representation, although any of the other forms could be used, as will become obvious.

To fix ideas, let us consider a neurogram of 6 elements, each of which may be 1 or 0 in the binary representation. These elements constitute a set, which may be arranged in 1-1 correspondence with a subset of the natural numbers. Such an arrangement orders the set, and we will designate its elements accordingly: 1, 2, 3, 4, 5, 6.

From this set a system of subsets may be generated, consisting of all possible combinations of the elements taken 1, 2,..., 6 at a time. The number of elements in a given subset is called the order of the subset. All subsets of a given order compose a class. Thus the members of the class of order 5 are 12345, 12346, 12356, 12456, 13456, 23456.

A "frame" of a particular binary neurogram, e.g., 101111, specifies a particular member of class 5, namely, 13456. It also specifies subclasses of order 4, 3, 2, and 1.

The relevance of this representation may be seen by considering the neuroanatomical phenomena of convergence and divergence.

A given neuron may, for example, receive inputs 12456. If the threshold of a neuron is defined as the number of excitatory inputs required to "fire" the neuron, and the threshold of a neuron is 5, the above-mentioned neurogram will not fire the neuron. If, however, the threshold is 4, the neuron will fire, since the subclass 4 of the frame is included in the "sorting function" (12456) of the neuron (see below).

The 1-1 correspondence with the subset of the natural numbers used to "order" the set is not the only ordering possible. We can also set up a 1-1 correspondence with a 2-dimensional array, for example, the matrix $\begin{pmatrix} 11, & 12, & 13 \\ 21, & 22, & 23 \end{pmatrix}$. We can also have n-dimensional orderings. Thus the set-theoretic representation of neurograms selectively exhibits the enormously rich capability of neural networks for transmitting and processing patterns of information.

The set-theoretic representation is not the only basis for "information coding" that is inherent in the properties of neural networks. Still another is the *symbolic* representation. In this scheme we assume that the sorting function of a "bank" of neurons is so structured that a relatively large size input frame "fires" a relatively small size output. Thus, an input (1011011011101) may correspond to an output (101). The output *symbolizes* the input according to a code, determined by the bank's structure and/or "state."

Finally the various mathematical representations so far considered are all subject to a variety of mathematical operations and transformations; in principle, almost any branch of mathematics is applicable. At least some of these operations may be embodied in neural networks. To provide for such a contingency, *the property-coded* representation is proposed. In this representation, our interest is not in the neurogram in explicit terms but in the value which some property of the neurogram may assume. A simple example of such a property in the frequency or channel representation might be the set of elements or channels whose frequency exceeds a given value. Another might be the set theoretic sum of the products of all pairs or elements in the binary representation.

$$P(N_t) = \cup A_i \cap A_j \qquad i \neq j$$

The property selected would depend on the relevant operation performed upon the property by the bank of neurons to which it is presented.

These, then, are some of the ways in which neurograms may be represented mathematically. Others are possible; indeed, it is plausible to state that almost any branch of mathematics may be applicable, and accordingly any representation suitable to the branch concerned is admissible. However, we have enough to start with, and it seems desirable now to consider the variety of neural operators that may be employed.

NEURAL OPERATORS

The neuroanatomical structure and neurophysiological mechanisms of a bank of neurons perform the equivalent of a variety of mathematical operations upon the input neurogram. In this section we shall consider some of these "neural operators." Before doing so, a few preliminary remarks and definitions are required.

By a bank of neurons we mean a collection of neurons which receives an input neurogram or set of neurograms from one or more sources and transmits an output neurogram or set of neurograms to one or more sinks. The sources may be receptor organs or other banks. The sinks may be other banks or effector organs.

A bank may contain one or more *internal sources* (neurogram generators independent of input or modulated by input). Such a bank is active. Otherwise banks are passive.

The term "bank" is used in preference to the neuroanatomical term "nucleus" in order to emphasize the fact that neurons widely separated in space may be part of the same bank. Just as a block schematic diagram differs from a wiring diagram of an electronic circuit, so will bank configurations differ from neuroanatomical structures. The criteria for assigning neurons to any given bank will be functional, not neuroanatomical.

Banks may be arranged into substructures, of which an infinite variety appear possible. We distinguish two types: tiers and loops. An *input* tier is the set of neurons receiving all inputs to the bank. A *secondary* tier is a set of neurons receiving neurograms from the input tier. An output tier is the set of neurons transmitting all outputs from the bank. A given tier may have synaptic connections with neurons within the tier.

A *loop* is a set of channels connecting the output of a tier back to a previous tier of the bank. Loops will be designated according to the tiers they connect. Thus loop 31 connects tier 3 output back to tier 1.

In addition to these (and possibly other) substructures, various operational configurations are possible, as illustrated in Fig. 1.

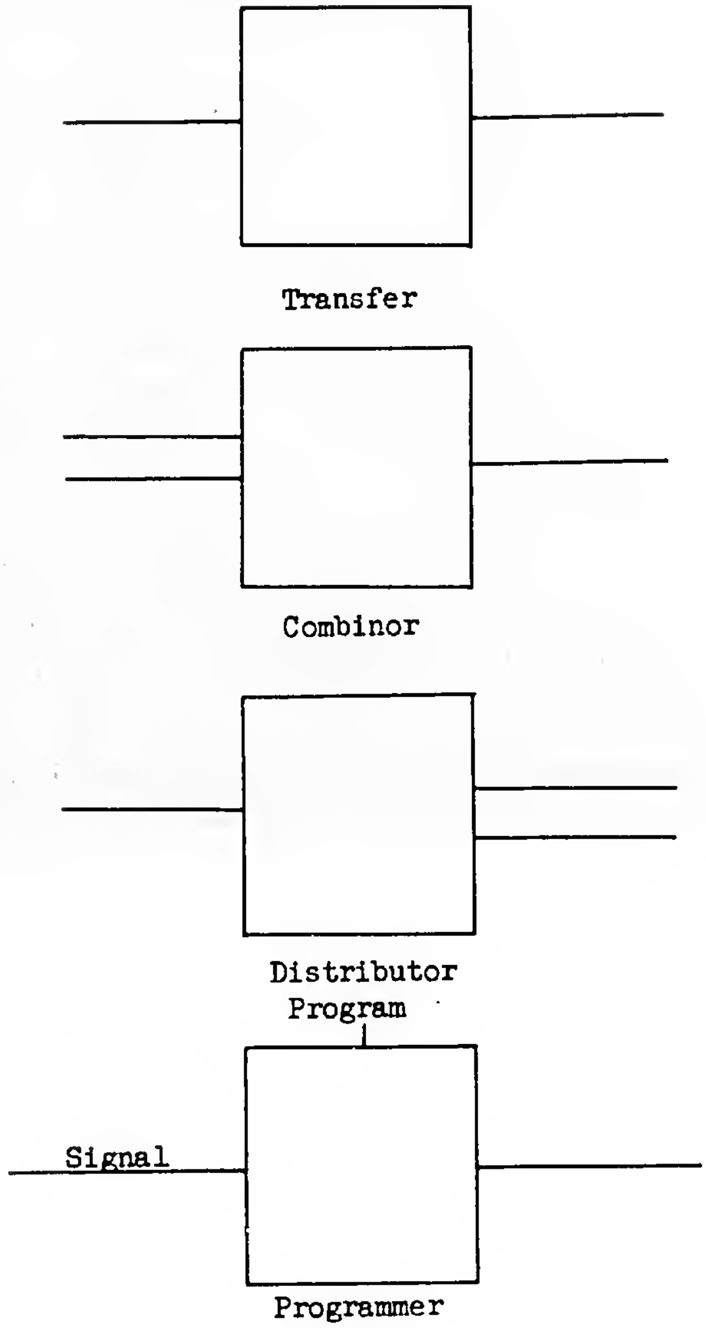


Fig. 1. Neural operator configurations

In transfer configuration a simple input neurogram is operated upon by the bank (or tier) to generate an output neurogram. Such operations as amplification, filtering, differentiation, integration, symbolic coding, or property coding illustrate uses of this configuration.

In combinor configuration two or more input neurograms are combined by a bank (or tier) according to some mathematical operation. Thus, for example, a weighted linear combination of inputs might be used. Another possibility is a set-theoretic figure gate. Suppose, for example, the input frame of a neurogram is represented by the elements (12378), and another by the elements (abcg). The first frame generates a class of subsets of order 3, only one member of which contains all neighboring elements (123). The same holds true of the second frame (abc). The sorting function of the bank may be so arranged as to fire an output if and only if both inputs contain at least one subset of three neighboring elements. The bank, in other words, functions as an "and" gate for these set-theoretic "figures."

In distributor configuration two or more outputs are generated by a bank (or tier) in response to a single input. Such a configuration might be used to transmit replicas of a neurogram to a variety of other banks (or tiers). It might also be used for "signal traffic control" operations, for example, synchronizing the activity of a number of different banks. (Such operations are analogous to "housekeeping" operations of a digital computer.)

In programming configurations one input provides a signal which is operated upon by the bank to produce an output neurogram. Another subthreshold input, the programming input, modifies the bank operator according to some "program." Thus, for example, the threshold might be changed from 6 to 3 excitatory inputs required to produce an output from a given neuron. Periodic fluctuations of threshold in response to a programming input could thus be used to provide a "sweep" through the ensemble of operations available to a bank.

Some of the basic mathematical operations performed by the neuroanatomical structures and neurophysiological mechanisms of a bank may now be considered (Coulter and McCulley, 1959). These may be represented in terms of five basic functions:

1. Sorting function
2. Excitation function
3. Residue function
4. Threshold function
5. Firing function

The sorting function represents the neuroanatomical properties of divergence and convergence (Lloyd, 1959) and the excitatory and inhibitory postsynaptic potentials (Eccles, 1957). As an axon approaches its termination it branches extensively, forming synapses with a number of different neurons. This phenomenon is called divergence. Conversely, each neuron receives synapses from a number of different axons, a phenomenon called convergence. Intracellular recording has shown that presynaptic impulses produce either a transient depolarization (excitatory postsynaptic potential) or hyperpolarization (inhibitory postsynaptic potential) of the postsynaptic membrane. Postsynaptic potentials sum algebraically, and, if sufficiently strong, produce an impulse which is transmitted along the postsynaptic axon.

Let us consider a particular postsynaptic neuron, and suppose it receives inputs from presynaptic axons labelled 1, 2, 4, 7, 9. Some of these will be excitatory, others inhibitory. In general, we can represent this by the set-theoretic relation

$$\alpha_i = \bigcup_{j=1}^{m} P_j A_j \quad ,$$

where

α_i = sorting function of neuron N_i,

A_j = the set of afferent elements,

P_j = "gating" operator,

P_j = +1 for excitatory effect,

P_j = 0 for no effect (no synapse), and

P_j = -1 for inhibitory effect.

In the example, $P_j = 0$ for $j = 3, 5, 6, 8$.

The sorting function for the bank (or tier) may be written

$$S = \bigcup_{i=1}^{n} \alpha_i = \bigcup_{i=1}^{n} \bigcup_{j=1}^{m} P_{ij} A_j \quad .$$

In the foregoing, we have assumed that an input axon terminates on only one synapse on a given bank neuron. Actually, many synapses are usually found. This can be taken into account in the sorting function by letting P_j assume integral values other than +1 or -1, corresponding to the number of synapses. For simplicity we will use gating operators, however.

The excitation function represents the degree of depolarization or hyperpolarization produced by a given binary frame of neurogram on a particular bank neuron. It is given by

$$E_i = \sum_{j=1}^{m} P_{ij} \; A_j \quad .$$

The influence of previous subthreshold excitation is represented by a residue function. Empirically, an exponential decay characterizes the time course of such activity (Eccles, 1957). We can represent this efficacy by a relation of the form

$$R_i(t) = \sum_{\tau=0}^{t} E_i(t - \tau)e^{-\beta\tau} \quad ,$$

where

$R_i(t)$ = residue function at time t of neuron i,

τ = time in discrete units (1 ms) from time, and t back to time 0

β = constant.

In addition to the influence of previous subthreshold excitation, variations in threshold associated with postsynaptic afterpotentials must also be considered. Such variations have the form of a slightly underdamped response of a second-order system to an impulse. They may be represented by a threshold function

$$\theta_i(t) = T_0 + \sum_{\tau=1}^{t} T' F_i(t-\tau)e^{-\gamma\tau} \cos \omega(\tau-1) \quad ,$$

where

$\theta_i(t)$ = threshold function at time t,

T_o = resting threshold function,

τ = time in discrete units (integral multiples of 1 ms) from time t back to time 0,

T', ω = constants, and

$F_i(t-\tau)$ = firing function at time $t-\tau$ (see below).

Finally, we must consider the firing function. This is essentially a decision function, having the value 1 or 0 according to the following:

$$F_i(t) = 1, \quad E_i(t-1) + R_i(t-1) > \theta_i(t-1)$$

$$F_i(t) = 0, \quad E_i(t-1) + R_i(t-1) < \theta_i(t-1) \quad .$$

These five functions by no means exhaust the mathematical operations potentially present in nerve nets. The possible role of field effects (Arvanitaki, 1942; Grundfest, 1959) has not been represented, nor have the roles of glial cells (Galambos, 1961) or "memory traces." They do, however, provide a basis for a highly complex and enormously varied manifold of operations of neural information processing. From this basis, by suitable combinations and admissable manipulations, we can construct neural operators capable of performing a remarkable variety of functions. In so doing we can make more explicit and precise the oft-made characterization of the brain as a computer; but it is likely that this will be accompanied by extension and enrichment of the meaning attached to the word "computer." In some ways the brain is like a digital, in others like an analog, computer; but these analogies appear superficial. We suggest that the brain may more accurately be characterized as a prototype of a more general type of system than has yet been envisaged, of which analog and digital devices are relatively simple special cases.

II. VISUAL DATA PROCESSING

INTRODUCTION

In studying information processing in the central nervous system, it was decided to be selective rather than comprehensive, since similar parts of the central nervous system have similar modes of operation imbedded in their organizational matrix. The visual system was selected as being representative of sensory systems. This is functionally the most important and has been most extensively studied.

The visual data processing system of man is a remarkably versatile system for processing information conveyed to the eyes by electromagnetic radiations from the environment in the narrow band of about 4.2 to 7.5 x 10^8 megacycles (420 to 750 teracycles). Its sensitivity range is about 50 to 60 db.

This system performs a variety of functions, some reasonably well understood, others vaguely discerned. An appreciable amount of data processing is performed by the retina itself. Other functions involve a variety of neural networks connecting components in widely separated regions of the brain. A block diagram of the system is given in Fig. 2. This should be regarded as an "organizational skeleton," not as a definitive schematic representation.

Of interest and considerable significance for the system is its dual input. Data from the left half of the visual field of each eye is processed in the occipital region of the right cerebral cortex, and vice versa. This results from the structure of the main visual pathway, as shown in Fig. 3. This dual input is of considerable importance in depth perception and certain other processes.

Visual data processing involves not only image formation by the eye, but also photochemical and neural processes in retina, and transmission and transformation of neural signals in the main visual pathway. Essential to many functions are the movements of the eyeballs and changes in pupil size and lens shape. The importance of these motor operations is not always adequately appreciated.

RETINAL DATA PROCESSING

Basic Structural Plan of Retina

The retina is far more than a sensory transducer; embroylogically and functionally it is part of the central nervous system. The neural signals leaving the retina via the optic nerve are already the result of a considerable amount of data processing.

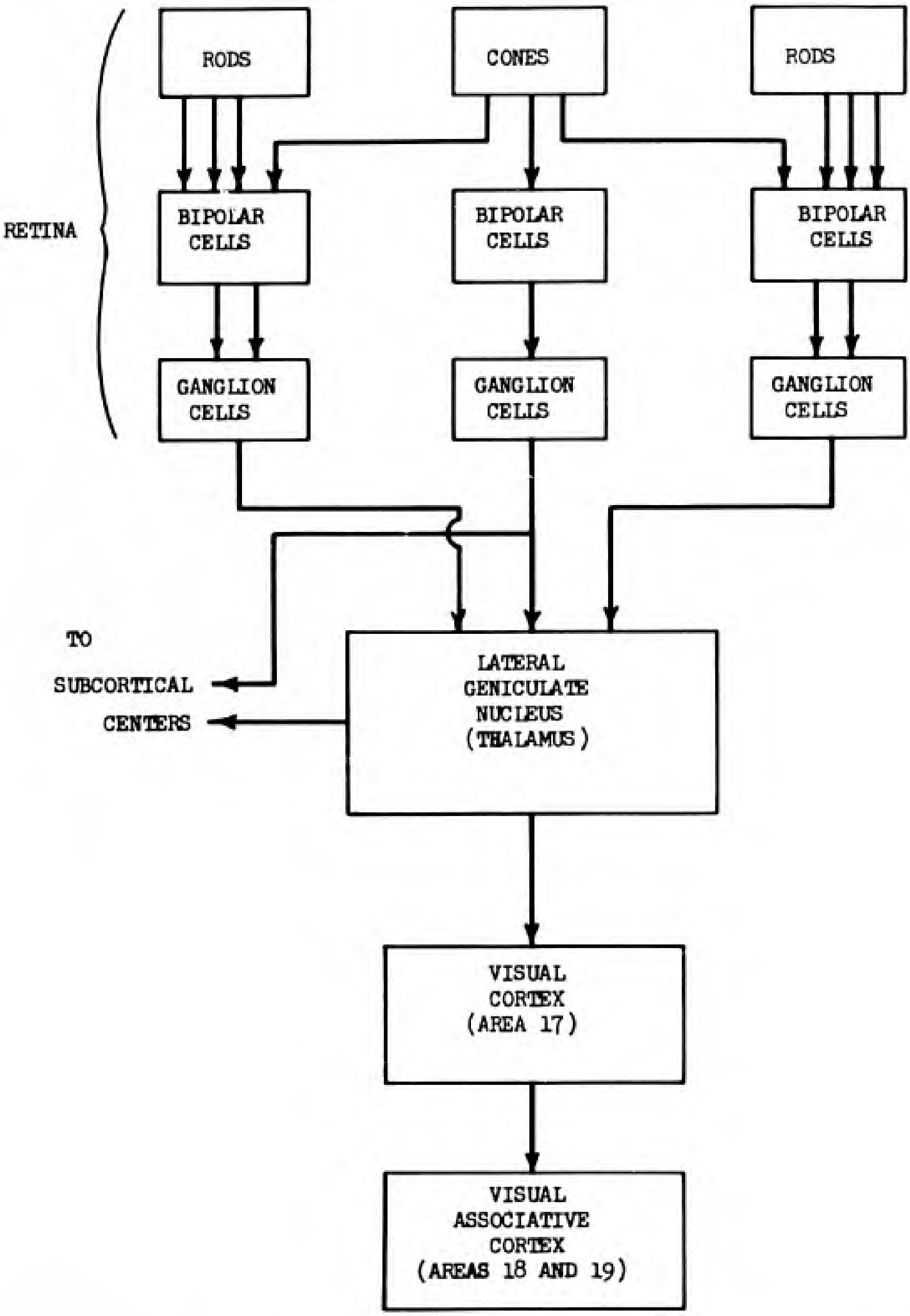


Fig. 2. Simplified block diagram of visual data processing system. (Several retinal cell types of uncertain function -- horizontal cells, amacrine cells, glial cells -- have been omitted.)

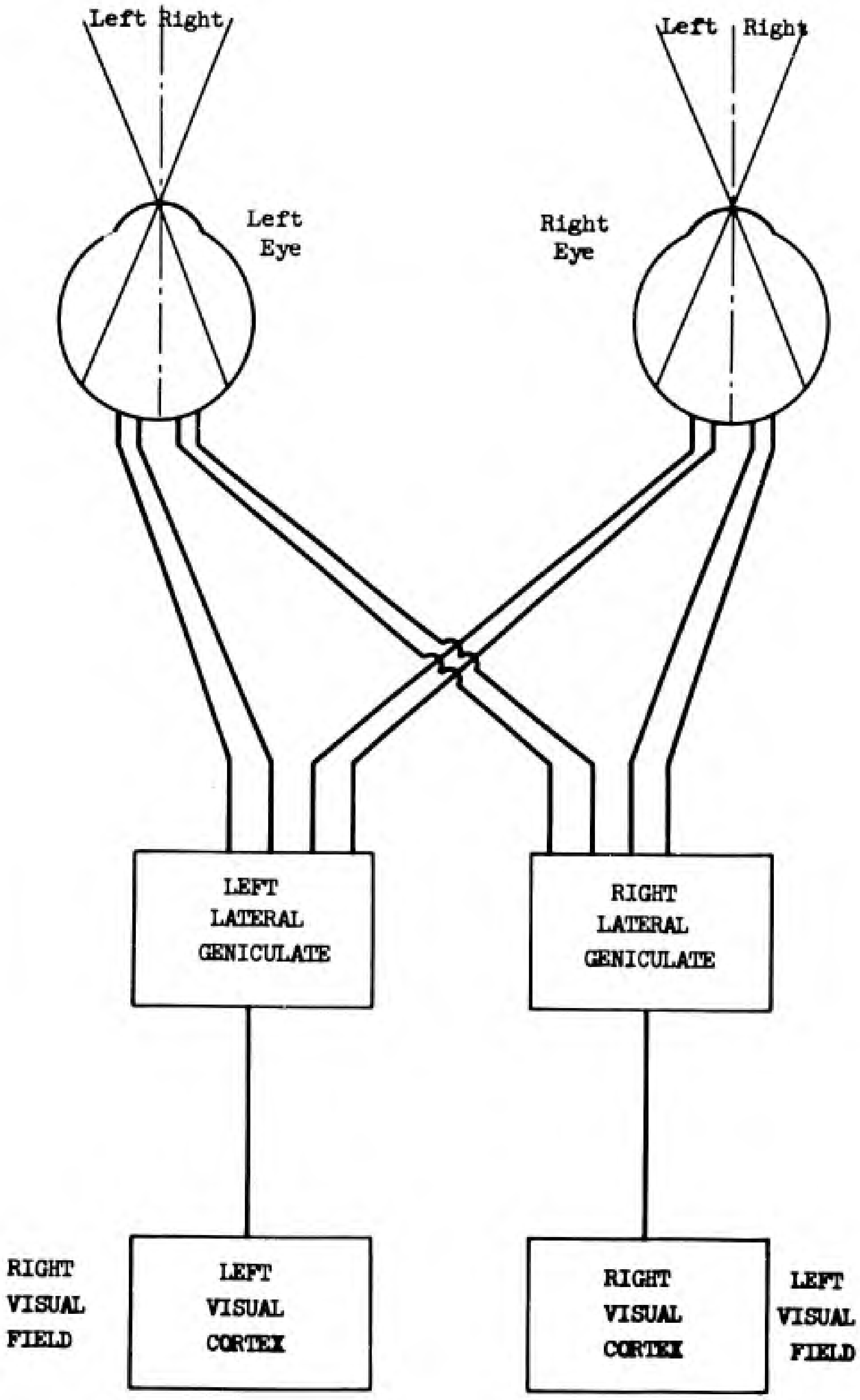


Fig. 3. Dual input organization of visual data processing system.

The sensory transducers of this system are the rods and cones. In man there are about 125-million rods and 4- to 7-million cones (Granit, 1959). These are illustrated in Fig. 4.

The rods are slender cells about two microns in diameter in the more central portions of the retina and four to five microns wide in the periphery. They contain a photosensitive pigment, rhodopsin. The rods, which give the retina its remarkable sensitivity, are highly responsive to very dim light. They are relatively insensitive to changes in wave length.

The inner ends of the rods synapse with bipolar neurons of the retina. Several rods synapse with each bipolar cell; in the more peripheral region several hundred may converge upon a single bipolar cell. This organization enables the rods to function as a light-collecting mechanism and amplifies their sensitivity (see Fig. 5).

The inner ends of the bipolar cells synapse with ganglion cells. The axons of these cells converge to the optic disc where they acquire myelin sheaths and leave the retina as part of the optic nerve.

The cones are thicker than the rods and are more centrally located. In the macula, an area of about 1 mm in diameter, there are no rods, only cones. The center of the macula is called the fovea; in this region the ganglion cells and other elements are displaced to one side permitting light to pass unimpeded to the cones.

It is widely believed that the cones contain three photosensitive pigments, corresponding to red, green, and blue wave lengths of light (Young-Helmholtz Theory). The evidence for this is still rather indirect* (Rushton, 1962), although some cone pigments have been isolated (Wald, 1959). The cones are far less sensitive to light than the rods, but have much higher capacity to discriminate differences in intensity. In the fovea each cone synapses with a single bipolar cell which in turn synapses with a single ganglion cell, giving, so to speak, a "private line" for central communication. In the peripheral macula, and in surrounding regions of the retina, there is a greater degree of convergence (see Fig. 6).

Also present in the retina, mostly between the receptors and bipolar cells, are horizontal cells providing lateral connections. These provide a basis for interaction among sensory channels, and may play a role in inhibitory processes.

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*Recently, Marks, Dobelle, and MacNichol (1964), in a preliminary report, presented direct evidence of three visual pigments in primate retinas.

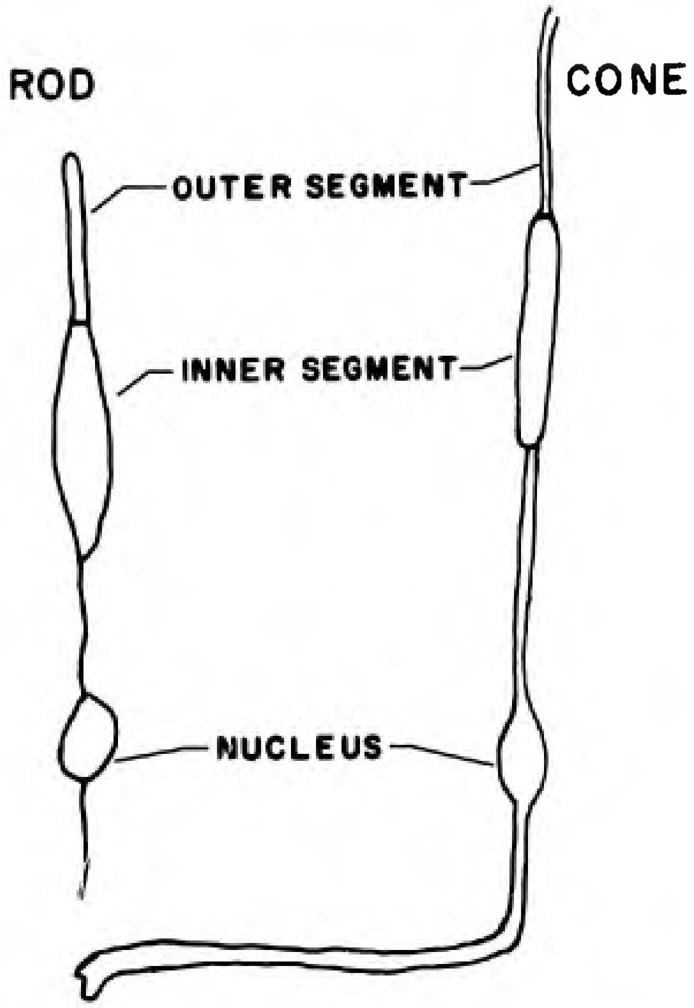

Fig. 4. Typical sensory transducers of retina (rod and cone cells). Diagrammatic representation from various sources.

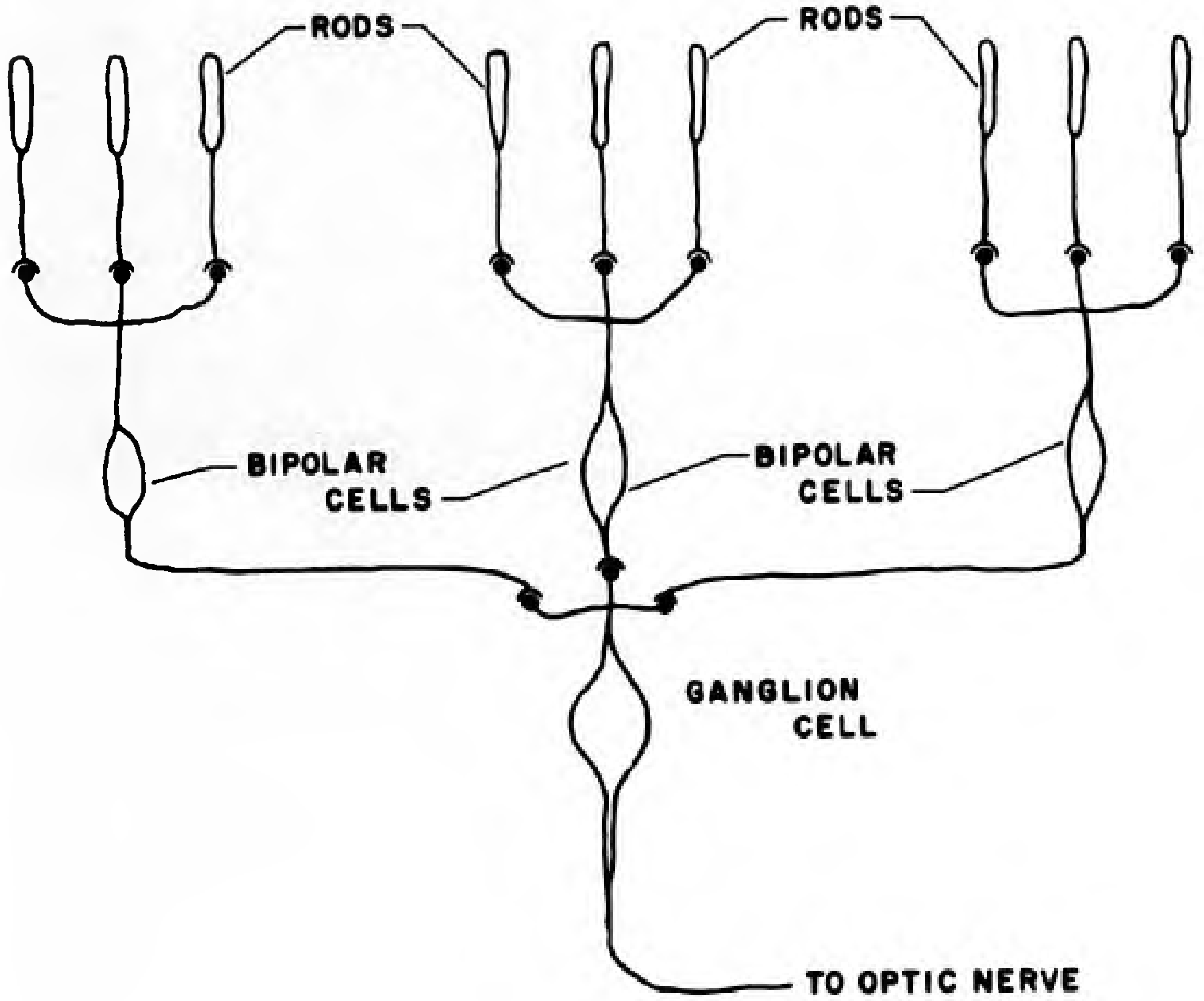

Fig. 5. Collection of light signals by peripheral retinal mechanism.

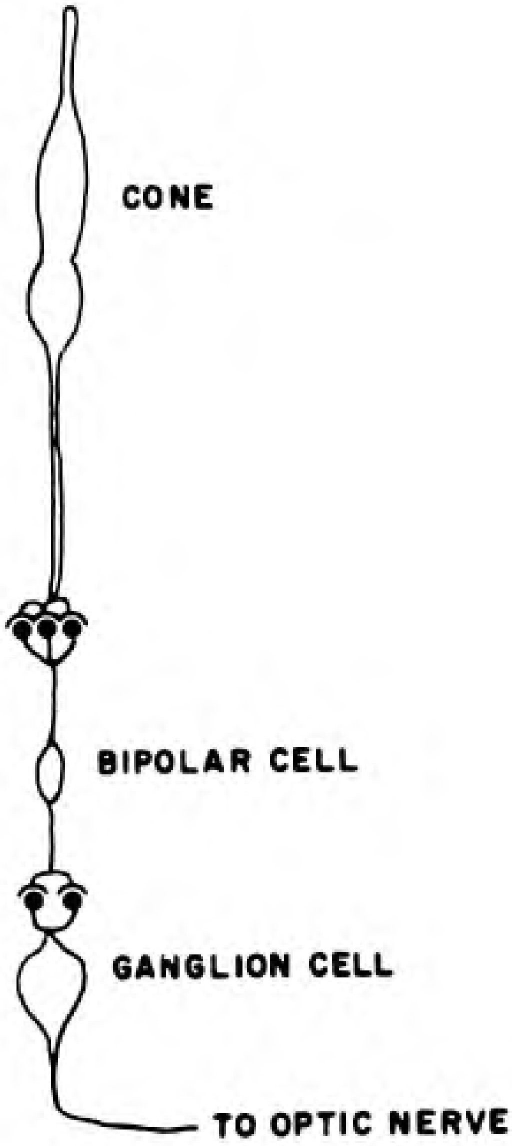

Fig. 6. "Private line" transmission of light signals from foveal cones.

Two other aspects of retinal histology deserve mention. The first is the widespread presence of glial cells. The second is the existence of efferent nerve fibers to the retina from some as yet unknown source in the central nervous system. Observed by Ramon y Cajal, these fibers terminate in the layer between the bipolar cells and the ganglion cells. These may facilitate or inhibit ganglion cell discharge (Granit, p. 709).

Form Detection

A great deal is known about the photochemical processes of vision (Wald). Very little is yet known about the processes by which photochemical changes are converted into neural signals (for a discussion of this problem, see Granit). However, a variety of studies have been made on the response of single units (presumably ganglion cells) and the impulse patterns they generate. From these studies the mechanism by which the retina detects the forms of visual images and signals their movement is becoming clearer.

If a tiny beam of light is focussed exploringly on the retina, and the activity of an individual neuron in the ganglion cell layer is detected with a microelectrode, the nerve action potentials associated with the light beam can be detected and recorded. This has been done most extensively in the frog retina (Hartline, 1938; Barlow, 1953; Lettvin *et al*, 1959) and in the retina of the cat (Kuffler, 1952).

Three types of response have been noted, as illustrated in Fig. 7. The first, called the "on" response, is an increased frequency of discharge when the light is turned on, followed by a decreased discharge frequency when the light is turned off. (It should be noted that in many cases these nerve cells fire "spontaneously," even in the dark. Some of this may be caused by stray light, but most spontaneous activity probably cannot be so explained. The significance of this "spontaneous" activity in the dark is not clear.)

A second type of response is called the "off" response. In this response, the frequency of discharge is decreased or cut off entirely when the light is turned on. A burst of impulses, followed by a return to a steady level, occurs after the light is turned off.

A third type of response is the "on-off" response. In this response there is an increased frequency of discharge when the light is turned on, decreasing to a steady, but still high, frequency as long as the light is on. Then, when the light is turned off, a second burst occurs, followed by a decay to a steady level.

A given type of response from a particular ganglion cell can only be obtained when the light beam is focussed within a relatively small area (at most a few hundred microns in diameter). This area is called a *receptive field*. These receptive fields may overlap; in terms of ganglion cell discharges, the retina can be described as an overlapping

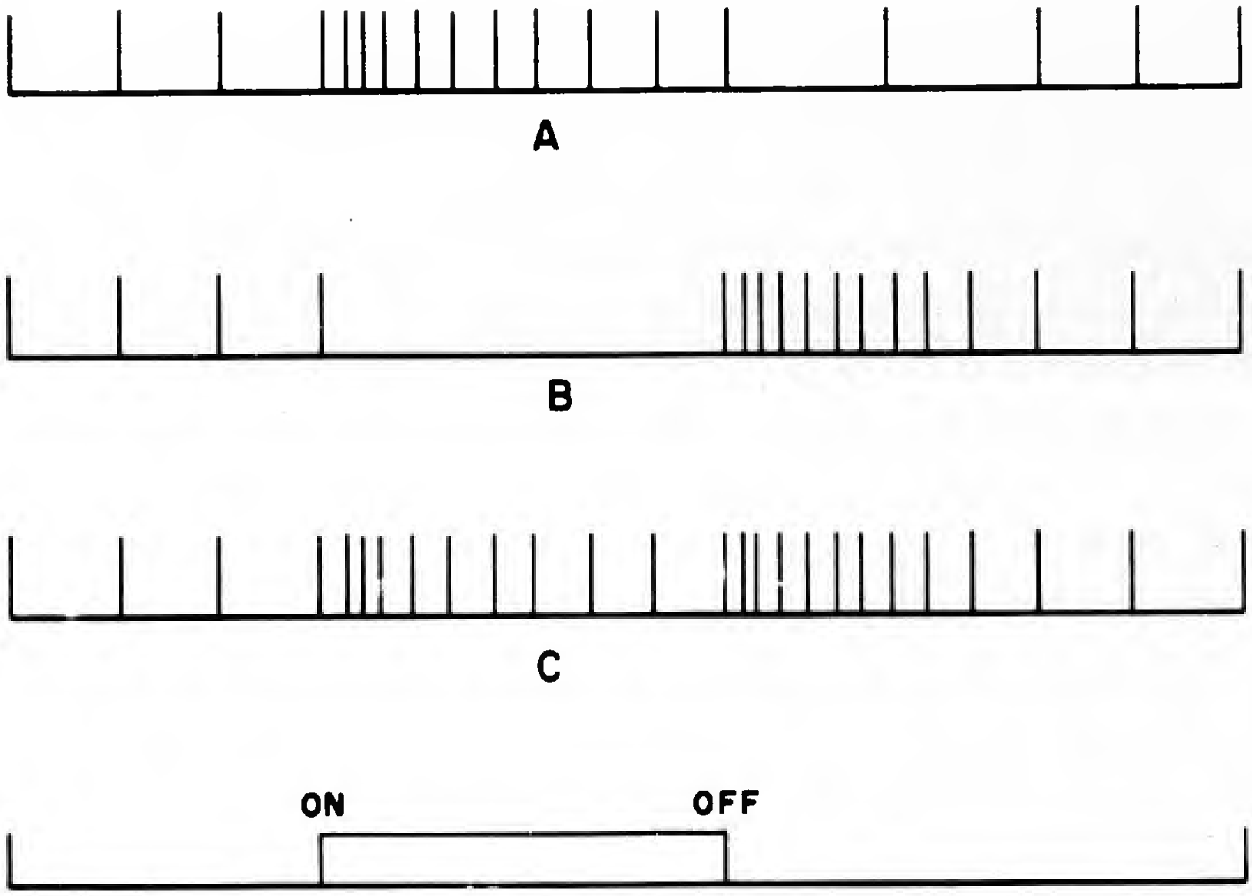

Fig. 7. Types of unit response in retina: A -- "On" response; B -- "Off" response; C -- "On-Off" response.

mosaic of receptive fields. It should be emphasized that this characterizes retinal function from one aspect only and should not be regarded as a complete characterization.

In the cat retina where this analysis has been carried further (Kuffler), a receptive field may yield an "on" response when the beam of light is directed to the center of the receptive field, but an "off" response when the light beam is directed to the periphery. At the intermediate zone, an "on-off" response may be obtained.

In other receptive fields an "off" response could be obtained when the exploring spot was in the center; an "on" response in the periphery. If two spots are used, focussed on different parts of the receptive field, the response could be converted from one type to another, depending on the location and relative intensities of the spots.

These studies show that the retina is not a system of discrete, independent channels, each of which transduces light intensities to neural impulse frequencies providing a faithful replica of the input signal. Rather, the retina appears to have been "designed by selection" to function (in part) as a form detector. (The same mechanisms may singularly well provide a highly selective, coded detection of movement, which will be discussed later.) The form of a simple image is determined largely by its boundary or contour. At the boundary, a sharp change in light intensity occurs. Such changes will be selectively detected by receptive fields organized as described above. Barlow has also shown how movement of a point across the retina will light up a trail of on-off sparks.

Lettvin, Maturana, McCulloch, and Pitts have investigated this problem further in studies on the frog retina and visual pathway. They classified retinal detectors into groups as follows:

Group I, the boundary detectors. These respond to any boundary in the retinal image, provided it is sharp. They do not respond to changes in overall level of illumination. They correspond to Hartline's "on" receptors.

Group II, the movement-gated convex boundary detectors. These respond only to boundaries that are curved (darker area convex) and that are moving or have recently moved. (They are admirably suited to the detection of flies and other small insects.)

Group III, the moving or changing contrast detectors. These have no enduring response but fire only if the contrast is changing or moving. They correspond to the "on-off" fibers of Hartline.

Group IV, the dimming detectors. These respond whenever the overall level of illumination is reduced. Boundaries play no role in the response.

Group V, unclassified. These relatively rare fibers fire at a frequency that varies inversely with the intensity level of illumination. There is no evidence that detectors of this type are present in the human retina; however, they are indicative of the type of organization that may be present.

Although form detection has been discussed as a retinal data process, this is not meant to imply that form detection occurs exclusively in the retina. There is evidence that additional data processing, significant for the detection of form, occurs at other levels of the visual pathway, and indeed that eye movements themselves play an important role.

Color Detection

Color vision is a complex process involving not only the retina but various other stations of the visual pathway. Here we shall be concerned with color detection (spectral discrimination) in the retina.

Color detection is generally believed to be associated with the cones. Simple evidence for this is the fact that colored light falling on the peripheral cone-free part of the human retina does not evoke the sensation of color.

It is well known that all the color hues can be produced by combinations of three monochromatic light beams: red, green, and blue. This has led to the assumption that there are three types of cone: one most sensitive to red, another to green, and a third to blue. The basic phenomena of color blindness can also be explained by this hypothesis. However, only recently have visual pigments (iodopsin and cynopsin) been isolated from cones. Correlations with the postulated three types of spectral sensitivity have yet to be established. The cone pigment of human cones has not yet been isolated.

Differences in spectral sensitivity of rods and cones -- known as the Purkinje shift -- are shown in Fig. 8. It has been found that the spectral sensitivity for rod vision correlates very well with the absorption spectrum for rhodopsin, the rod pigment. The absorption spectrum of iodopsin also correlates with the spectral sensitivity for cone vision. This indicates that the photochemical properties of the visual pigments are primarily responsible for the spectral sensitivity characteristics of rod and cone vision.

The process by which light beams of different wavelength are converted into impulse patterns in the optic nerve has been studied by Granit and others. Granit found two types of spectral sensitivity: broad-band types, called dominators, responding about equally over the visible spectrum; and narrow-band types, called modulators, responding over much narrower regions of the spectrum, as indicated in Fig. 9. In general three "regions of predilection" have been found in various types of retina, definable in terms of the wavelength of maximum sensitivity.

Whether the modulator curves reflect the spectral selectivity of different cone pigments or whether they are the result of information processing in the neural networks of the retina, is not yet understood.

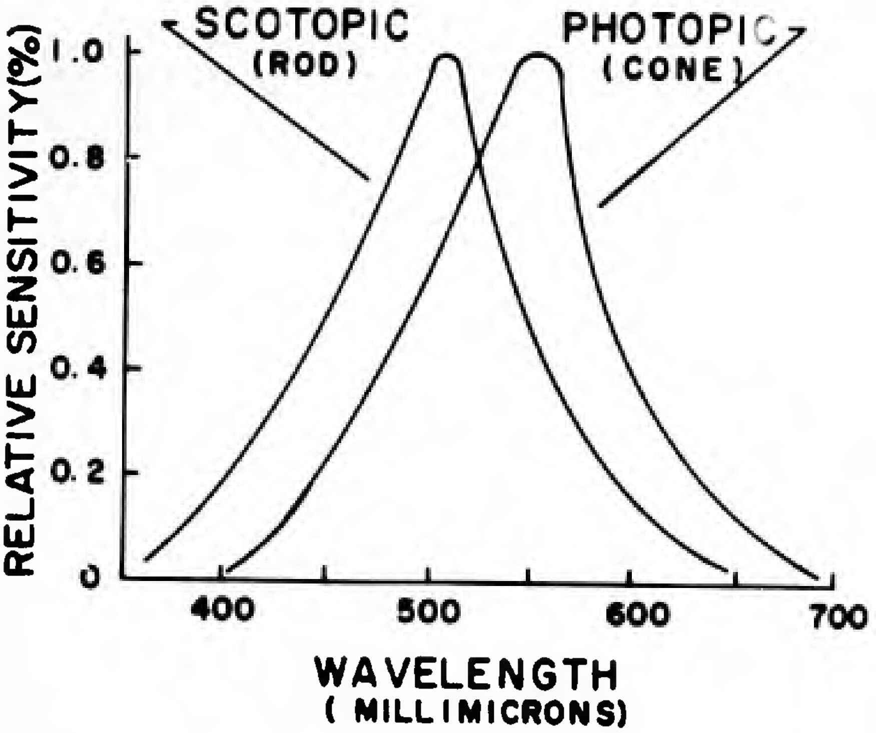

Fig. 8. Spectral sensitivity of rods and cones.

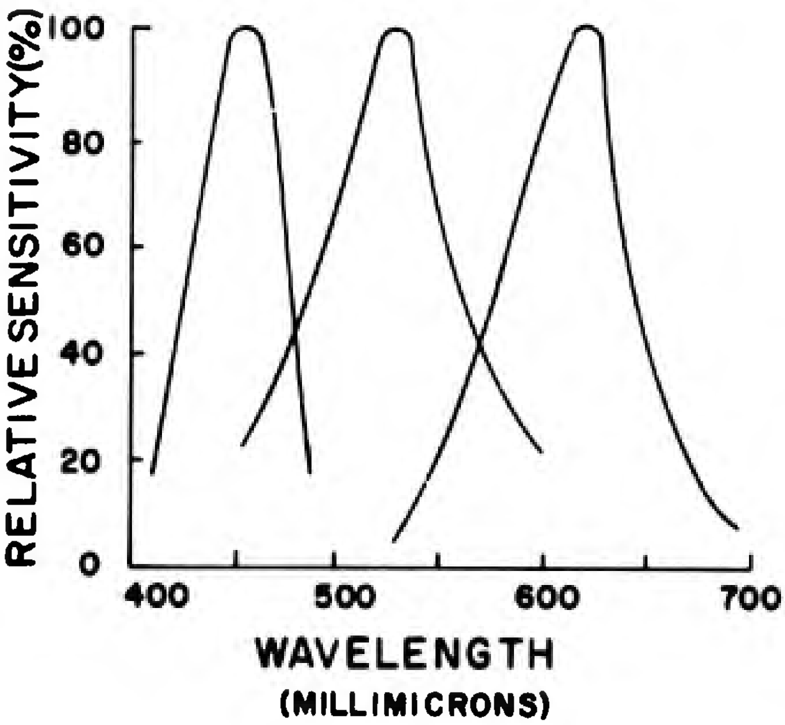

Fig. 9. Spectral sensitivities of "color sensitive" mechanisms of retina -- modulator responses (after Granit).

Color detection (spectral discrimination) is but one of the processes involved in the complex phenomenon of color vision. Higher centers in the visual pathway participate to a considerable degree, as shown by the simple experiment of observing a white object with a green filter in front of the left eye and a red filter in front of the right eye; the resulting sensation is yellow. It is natural to assume that the more complex processes of color vision require the participation of higher centers, but our knowledge is not yet sufficient to enable us to say how much of the data processing involved is performed in the retina itself.

The Detection of Movement

The mere fact that an image moves across the retina does not necessarily result in the perception of an object in motion. Since change in position of a retinal image can be produced in two ways -- by movement of the object or of the eyeball -- there must exist some mapping system whereby the effects of eyeball movement are distinguished from the effect of object movement.

Of interest in this context is the observation (Whitteridge) that attempts to move the eye by means of a paralyzed muscle (normal eye covered) result in an apparent displacement of the visual field in the direction of the intended movement. For example, if an attempt is made to move the left eye to the left when its left lateral rectus muscle is paralyzed, the observer reports that the visual field is apparently displaced to the left.

These phenomena indicate that the detection of movement is by no means a simple process. All that the retina alone can do is to detect changes in position of the retinal image. For this, the aforementioned responses of receptive fields to changes in light intensity distribution appear to be of basic importance. The means by which movement of an image is signalled is still not well understood, however.

Several problems present themselves. First, why is a movement perceived as a movement of an object, and not as a succession of images at different sectors of the visual field?

This problem is closely related to the problem of "flicker fusion" discussed below. At a given region of the retina and average intensity of illumination, a stationary flickering image will appear without flicker (flicker fusion) above a certain critical flicker frequency. If the image shifts position from one flicker to the next, it is perceived as moving (above the critical fusion frequency). However, the change in position cannot exceed a certain maximum else the image will not appear as moving continuously but as "jumping" (disappearing and reappearing).

Second, when an image is detected as "moving," eye movements ("pursuit" movements) occur which tend to shift the image to the fovea and to keep it there. Such a process involves not only detection of image displacement -- which can be done by the retina -- but also discrimination of this from eyeball movement, and the reflex genesis of a control signal to produce eyeball movement of the correct direction and amount. In lower vertebrates the superior colliculus appears to be the primary computer for effecting this process; in mammals, including man, the visual cortex also is involved, perhaps primarily.

The role of the retina in these processes is necessary but not sufficient. The "movement-detector" of the frog retina has not yet been demonstrated in mammalian retinas, which otherwise must provide the necessary information via serial excitation of receptive fields.

Temporal Continuity of Visual Objects: Flicker Fusion

If a very brief flash of light is focussed on the retina, the retinal response persists after the light is turned off. This is not a manifestation of the "off" response since it can be produced in the "on" response areas. Rather, it is a reflection of the time required for retinal processes to occur, and the fact that the time course of these processes is largely determined by the properties of the retina, not the stimulus.

If a flickering light is focussed on the retina, retinal processes may wax and wane as the light alternately becomes brighter and dimmer -- provided the flicker is relatively slow. As flicker frequency increases, eventually a point is reached beyond which retinal processes are unable to follow the flicker, but remain virtually in a steady state. This is known as flicker fusion, and the minimum frequency at which it occurs is the critical flicker frequency (CFF).

There are two chief ways* in which the critical flicker frequency may be determined. One is psycho-physical, in which a human observer reports when a flickering image is seen without flicker as the flicker is gradually increased by the experimenter. This method is quite sensitive and reproducible, but it involves other parts of the visual pathway besides the retina.

The second way is by use of the electroretinogram. Here a flickering light produces a periodic complex electrical waveform, with fusion occurring at frequencies comparable to those determined psychophysically.

Flicker fusion depends primarily on two things: the intensity of illumination, and the type of receptor stimulated.

For a given receptor type the frequency of flicker fusion increases with increasing intensity of illumination. The relationship is approximately logarithmic over a large range; that is, the critical flicker frequency increases as the logarithm of the intensity of light.

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*A third way is by observing the response of individual units to flickering light. This is technically more difficult but yields results similar to those described.

As might be expected, cones are more able to "follow" flicker to higher frequencies than are rods, under most conditions. The critical flicker frequency at low levels of illumination is determined by rods, and may be as low as five or six per second. At high levels of illumination, the critical flicker frequency is determined by cones, and may be as high as 50 - 60 per second.

Above the CFF, fluctuations of image intensity are not detected by the retina; the perceived image is endowed with temporal continuity. Where intensity fluctuations are concerned the retina appears to act as a low-pass filter with variable cut-off.

IMAGE SELECTION

Data Processing in the Visual Pathway

A remarkable capability of the visual pathway is the relatively small number of channels used to transmit retinally processed information. According to Polyak, man has 3-6 million cones and 125 million rods, but only about one million optic nerve fibers (an unknown but probably small fraction of which are centrifugal).

This implies a considerable amount of retinal data processing. We still have a relatively small degree of understanding of the nature of this processing, other than the relatively crude correlations between stimulus attributes and impulse patterns in retinal ganglion cells, as previously described. Modern emphasis on microelectrodes and single fiber techniques, while providing much valuable information about mechanisms, tends subtly to distort our views in the direction of ignoring the activity going on in other ganglion cells, or in other parts of the retina.

It is possible that the retina employs a kind of multiplex in the transmission of neural signals to higher stations of the central nervous system. We have no conclusive evidence for this, but the high degree of convergence from receptor elements to ganglion cell axons suggests the possibility that a given axon may serve as a common channel for a variety of sensory signals. The "off" response is thought by some to be the neural basis for the sensation of black and by others to be basic for the mechanism of contrast, boundary detection, movement detection, etc. It might indeed be all of these things; but it might also be the manifestation of a process of transmitting previously stored information during periods of receptor inactivity.

If a kind of multiplex is used, the question arises as to how different neural signals carried by a common channel are sorted out in higher stations of the visual pathway. One way in which this might be done is by the set of neighboring axons in which signals are simultaneously occurring. To illustrate, let us designate a set of five neighboring axons by 1,2,3,4,5. If an impulse (or short burst) in axon 1 is accompanied simultaneously by activity in axons 2 and 3, this would identify one signal. At a later time axons 1, 4, and 5 might be simultaneously excited, identifying another signal. If at the higher receiving station axons 1, 2,3 go to neuron a, and axons 1,4,5 to neuron b, both having a threshold of three, i.e., both requiring simultaneous activity in three inputs in order for firing to occur, the signals could thereby be sorted out. Such a sorting code is analogous to pulse code modulation, except that the spatial position of an impulse in a set of axons, rather than temporal position in a pulse train, is used to encode information.

No such "neural multiplex" has yet been demonstrated; but the capability is there, and it would provide a means whereby the same channel could transmit different kinds of information -- such as color or intensity. From a bionic standpoint, the equivalent of this type of multiplex might be worth examining.

No matter how information is transmitted in the optic nerves, it is received by the lateral geniculate nuclei of the thalamus, the next station on its way to the visual cortex. The lateral geniculate nucleus has several striking characteristics. In the monkey and man, it is organized into six layers. Three of these layers (1, 4, and 6) receive fibers only from the contralateral retina. The other three layers (2, 3, and 5) receive fibers only from the ipsilateral retina. There is no intermingling of the fibers from the two retinae (Glees, 1961).

This fact is of interest since it indicates that there is no neuroanatomical basis for binocular fusion at this level in primates. This is not the case in the cat, where interaction of impulses from the two eyes has been demonstrated (Fillenz, 1961). This is an illustration of the tendency for functions to be transferred to the cortex in higher animals, a tendency amply documented in many other ways.

A second fact of interest is that the number of output fibers from the lateral geniculate body is about equal to the number of input fibers from the retina (about a million for the two nuclei). Furthermore, there is no evidence of the existence of interneurons in the lateral geniculate nucleus. According to Glees, there is some divergence in the distribution of optic nerve fibers, each optic nerve fiber being in contact with more than one and probably more than five cells in the lateral geniculate nucleus.

The fibers from the retina are not the only inputs to the lateral geniculate nucleus, however. Arden and Sorderberg (1961) have recently shown that activation of the brain stem reticular formation can increase or decrease the firing rate of cells in the lateral geniculate body. Thus the reticular system has the ability to modify visual signals on their way from retina to visual cortex.

Arden and Sorderberg conclude that the lateral geniculate seems to act as an interpreter, a recorder, and a mixer of retinal information. How it does these things remains to be determined; it certainly is more than a mere relay station. Barlow (1961) has advanced the interesting hypothesis that the sensory relays recode sensory messages so as to reduce redundancy without loss of information.

On their way to the lateral geniculate nucleus, some fibers of the optic tract branch off. These fibers go to two nuclei in the brain stem called the pretectal nucleus and the superior colliculus. They are involved in the light reflex and other visual reflexes discussed below.

From the lateral geniculate mucleus, visual information is transmitted to the visual cortex. In man, this lies mostly on the medial aspect of the cerebral hemisphere in the occipital region, located above and below a large fissure called the calcarine fissure. Part of the visual cortex also extends over the occipital pole to the lateral aspect of the cerebral surface.

The central part of the retina, the macula, is projected upon the posterior part of the visual cortex, and the peripheral part of the retina upon the anterior part. As might be expected, the macular portion of the visual cortex is relatively large, taking up a much larger fraction of the visual cortex than the macula itself does of the retina.

As indicated above, the left half of each visual field is projected to the right cerebral hemisphere, and vice versa. Complete destruction of the visual cortex on one side thus leads to blindness of the opposite visual field. However, lesions that do not produce complete destruction may spare macular vision, to a considerable degree, at least.

Surrounding the visual cortex (called area 17 by neuroanatomists) is another area associated with vision, area 18. Surrounding area 18 is still another having visual functions, area 19.

Recently the response of single neurons in the visual cortex has been extensively studied (Akimoto and Creutzfeldt, 1957; Von Baumgarten and Jung, 1952; Baumgartner and Hakas, 1959; Grusser and Cornehls, 1959; Hubel and Wiesel, 1962; Jung, 1961). A variety of different types of activity was found in response to binocular stimulation by diffuse light. The cortical neurons were classified into five types as follows:

Type A - No response

Type B - Excitatory response to "on"
Inhibitory response to "off"

Type C - Inhibitory break for both "on" and "off"

Type D - Inhibitory response to "on"
Excitatory response to "off"

Type E - Delayed excitatory response to "on"
Excitatory response to "off"

It was also found that neurons of the visual cortex receive inputs from vestibular neurons and from the nonspecific reticulothalamic system.

Neurons responding to nonspecific thalamic stimulation were also divided into five types, distinguished by their different patterns of activation or inhibition. The latencies of response were longer and more variable than the response to stimulation by light. There was no statistical correlation between these responses and responses to light stimulation. However, most neurons of the visual cortex were found to receive convergent impulses from retinal, nonspecific reticulothalamic, and vestibular afferents.

Four types of response were found to labyrinthine stimulation by polarizing currents:

Type α - No response (rare)

Type β - Activation by onset only

Type γ - Activation by cessation only

Type δ - Activation by both onset and cessation

These results indicate that the visual cortex is not only a visual data processing center, but also that it is a coordinating center utilizing data from vestibular neurons and thalamic reticular system neurons as well. It has been suggested (Jung) that the vestibular information is used to stabilize visual space with relation to movements of the head. The role of nonspecific thalamic neurons may be related to shifts in visual attention.

In addition to responses to diffuse light described above, recent studies have also been made of the response of visual cortical units to light patterns (Hubel and Wiesel, 1959; Baumgartner, 1962; Baumgartner and Hakas, unpublished, quoted in Jung, 1961).

We shall follow primarily the treatment by Hubel and Wiesel who found, first of all, that many cortical units which showed no response to diffuse light showed a response to patterned light. This means that the type A neuron of Jung may play an important role in the detection of visual patterns and their movement. Other of Jung's types may also be so involved. Hubel and Wiesel made no attempt to classify neurons according to response to diffuse light, at least in this study.

A remarkable variety of types of response was found. Hubel and Wiesel classified visual cortical neurons into two basic groups, according to the properties of their receptive fields. The first group, termed "simple," gave responses that could be interpreted in terms of the arrangements of excitatory and inhibitory regions of their receptive fields. In other words, when their receptive fields had been mapped with small spots, the response of the neurons to visual patterns (slits, edges, etc.) could readily be interpreted in terms of their response to small spots.

The second group, called "complex," gave responses which bore little obvious relationship to the response to small spots. The responses of complex neurons to visual patterns could be interpreted as the result of combinations of responses of "simple" neurons, however. The hypothesis was advanced that the "complex" neurons received inputs from two or more "simple" neurons.

In contrast to the receptive fields of retinal and geniculate neurons, which were organized in circular scheme ("on" center-"off" periphery, and "off" center-"on" periphery), the receptive fields of cortical neurons exhibited linear schemes of organization. Thus, for example, one type gave "on" responses along a straight line (or narrow band), with "off" responses in the exterior regions of the field. The axis of the receptive field was characteristic of each cortical cell, and might be vertical, horizontal, or oblique.

"Simple" cortical neurons were classified as follows (illustrated in Fig. 10):

(a) Symmetrical flanks
    (1). Excitatory centers
    (2). Inhibitory centers
(b) Asymmetrical flanks
    (1). Excitatory centers
    (2). Inhibitory centers
(c) Large inhibitory centers with narrow excitatory flanks
(d) One excitatory region and one inhibitory ("edge" type)

In all such neurons the orientation of the receptive field was critical. A change of the axis by 5-10 degrees was usually enough to reduce a response greatly or to abolish it entirely. These neurons responded not only to stationary patterns but to moving patterns as well; indeed, moving stimuli were very effective. The response varied with the rate of movement, an optimum rate being associated with each cell.

"Complex" neurons, as noted above, were cortical neurons which responded to stationary or moving forms in ways that could not be predicted from maps made with small circular spots. In many cases such maps could not even be made, since the response was mixed or small. Such cells did, however, give characteristic responses to visual patterns. They were classified by Hubel and Wiesel as follows:

(a) Activated by slit - non-uniform field

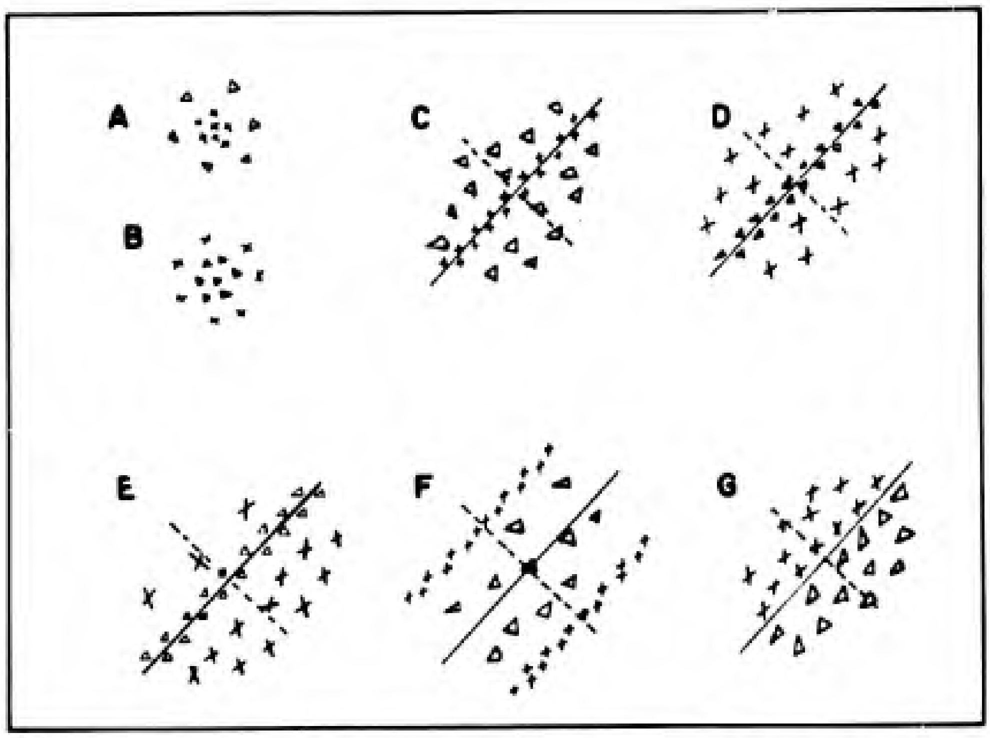


Fig. 10. Types of lateral geniculate and cortical receptive field. Pluses are "On" sites; triangles are "Off" sites. (A) On-center geniculate field. (B) Off-center geniculate field. (C) "On" axis with "Off" flanks. (D) "Off" axis with "On" flanks. (E) Asymmetrical field, "Off" axis with "On" flanks. (F) Large central "Off" zone with narrow "On" flanks. (G) Excitatory region with linear boundary adjoining inhibitory region. (After Hubel and Wiesel).

(b) Activated by slit - uniform field

(c) Activated by edge

(d) Activated by dark bar

The first type characteristically showed an "on" response when the slit was in one half of the receptive field; an "off" response when the slit was in the other half. Orientation and width of the slit were quite critical.

The second type characteristically gave an "on-off" response everywhere in the receptive field, provided the slit was oriented parallel to the receptive field axis. Orientation and width of the slit were critical. These neurons were quite responsive to moving stimuli, provided orientation was maintained.

The third type characteristically gave an "on" response to an edge; that is, to a field consisting of a bright area on one side and a dark area on the other with a sharp boundary between. If the field was reversed -- dark area changed to light and light to dark -- an "off" response was observed. Changes in orientation of the edge markedly reduced the response. Changes in position had little effect if the orientation was unchanged.

This type of neuron was similar to the "edge"-type simple neuron described above. The chief difference was that the position of the edge could be changed over a wide area without significantly changing the response, so long as the orientation of the edge was unchanged. On the other hand, the position of the edge for the "simple" neuron was critical.

A fourth type of complex neuron was the "dark bar" type. This type characteristically gave an "on" response to a visual field which was uniformly bright except for a dark bar in a particular orientation, e.g., horizontal. A change in orientation quickly extinguished the response. On the other hand, changes in position of the dark bar did not abolish the response. Another feature was strong discharge when the bar was moved in a particular direction, e.g., slowly downward. Movement in other directions or rapid movements in any direction gave weak or negligible responses.

Hubel and Wiesel suggest that the simple cortical receptive fields represent the first, or at least an early, stage in the modification of signals from the geniculate nucleus. A possible scheme for this organization is shown in Fig. 11.

Similarly, the complex cortical receptive fields may represent a higher order of information processing in the visual cortex combining outputs from several "simple" neurons, as shown in Fig. 12.

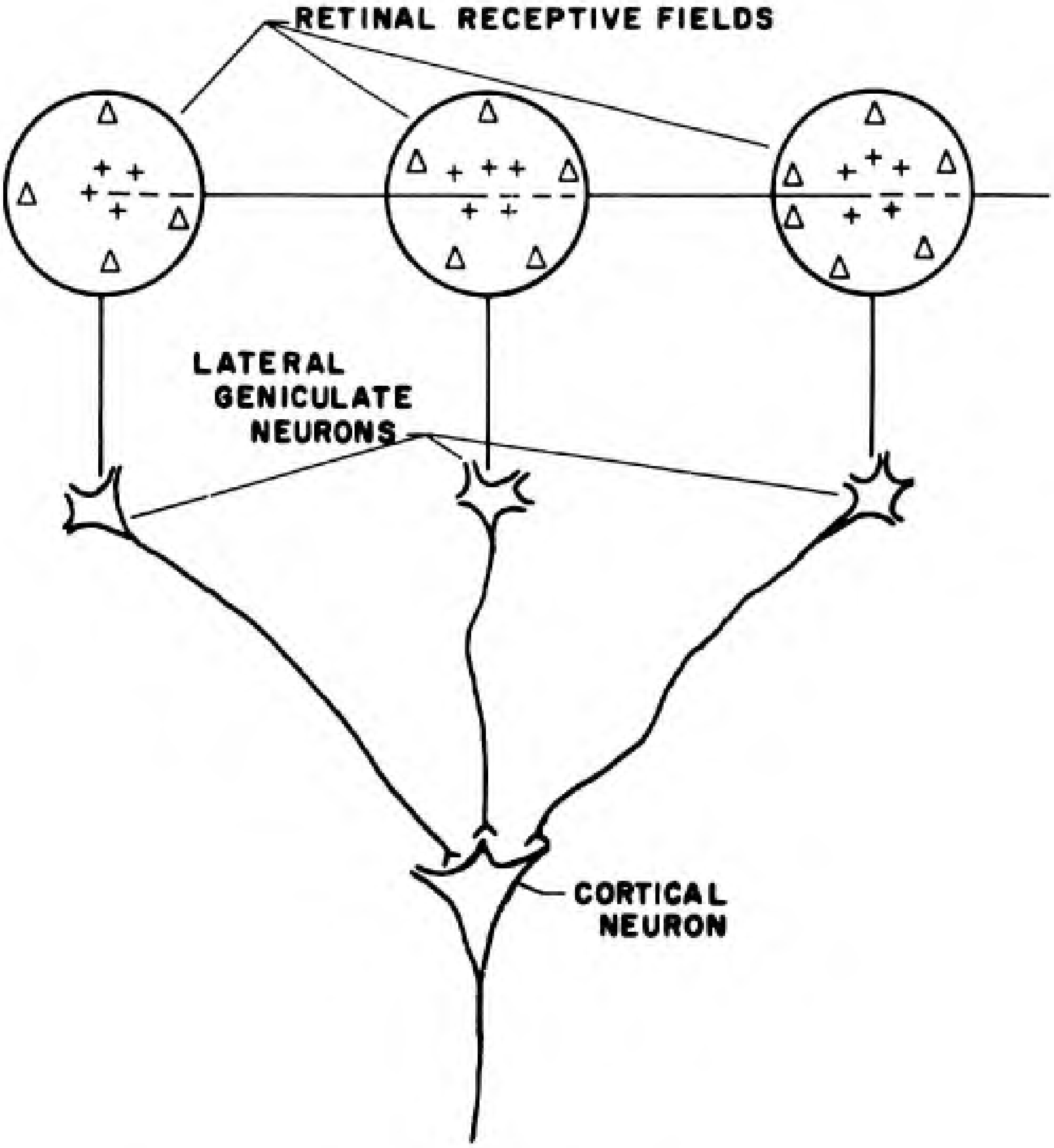


Fig. 11. Neural network for simple receptive fields (hypothetical). The field represented is shown in C, Fig. 10; "On" axis with "Off" flanks. The retinal fields have "On" centers arranged along a straight line on the retina. (After Hubel and Wiesel).

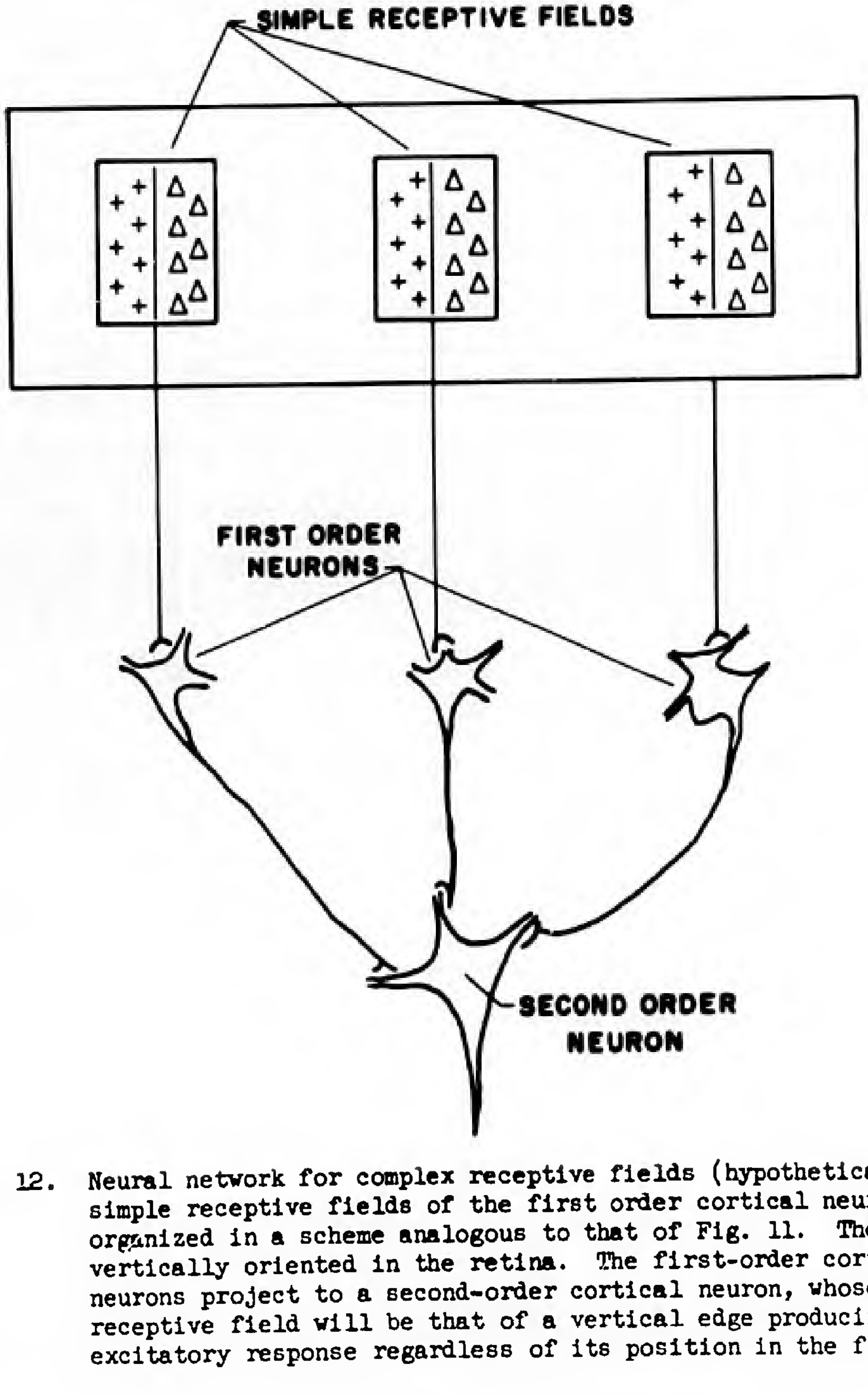


Fig. 12. Neural network for complex receptive fields (hypothetical). The simple receptive fields of the first order cortical neurons are organized in a scheme analogous to that of Fig. 11. They are vertically oriented in the retina. The first-order cortical neurons project to a second-order cortical neuron, whose complex receptive field will be that of a vertical edge producing an excitatory response regardless of its position in the field.

The visual cortex thus shows an organization for visual information processing that is remarkably well suited for the detection of forms, irrespective of position or orientation, and for the detection of movement, as that of a moving object whose properties are invariant under spatial transformations.

Estimates of the number of neurons in the visual cortex (area 17) are difficult to ascertain, probably because there are so many potential sources of error. Krieg (1953) estimates the total number of cortical neurons at 13.5-billion, with an estimated volume of 560 cc. This gives an average overall density of 2.4×10^7 neurons per cc. Crosby et al. (1962) quote estimates of the visual projection area at 20.4 to 45 sq cm, with an estimated average width of 1.5 to 2.2 mm. From these data, an estimated range of 7.3×10^7 to 23.8×10^7 neurons in the visual cortex can be derived.

Surrounding the primary visual cortex (area 17) is another region (area 18) primarily concerned with visual functions. We know much less about its function and organization than we do about area 17. Area 18 does receive extensive projections from area 17; and in turn projects to the surrounding area 19, to the contralateral area 18 via the corpus callosum, and to auditory, somesthethic, motor, prefrontal, insular, and temporal tip regions of the ipsilateral cortex, via the long association bundles of the hemisphere. Area 18 also projects to the midbrain optical centers and receives some inputs from the pulvinar, a thalamic nucleus. Some of these interconnections are shown in Fig. 13.

In man, total blindness follows bilateral destruction of area 17. A patient with an intact area 17, but with extensive destruction of area 18 will walk around a ladder (indicating that he sees it) but be unable to name it or tell its use. Clinically, this condition is sometimes known as visual agnosia.

Stimulation of area 18 during neurosurgical procedures in man produces visual images such as stars, wheels, or streaks of light. Patients with irritative lesions of area 18 may report visual hallucinations. These data collectively suggest that area 18 is primarily concerned with interpreting the significance of visual objects, and have led to its designation as a visual association area.

In several mammals, including the monkey, a second visual area has been described, occupying the border region between areas 17 and 18. In the rabbit, it is reported to show a pattern which is the mirror image of that on the primary visual area. Its functional role is not clear.

Area 18 is also believed to function in association with area 19 in connection with following eye movements and fixation, discussed below.

Image Fixation

One of the most remarkable attributes of the visual data processing system is its capacity to select an object, detected in the field of vision, for primary consideration, and by eye movements to fix the image of that object upon the most sensitive and discriminative part of the retina -- the fovea.

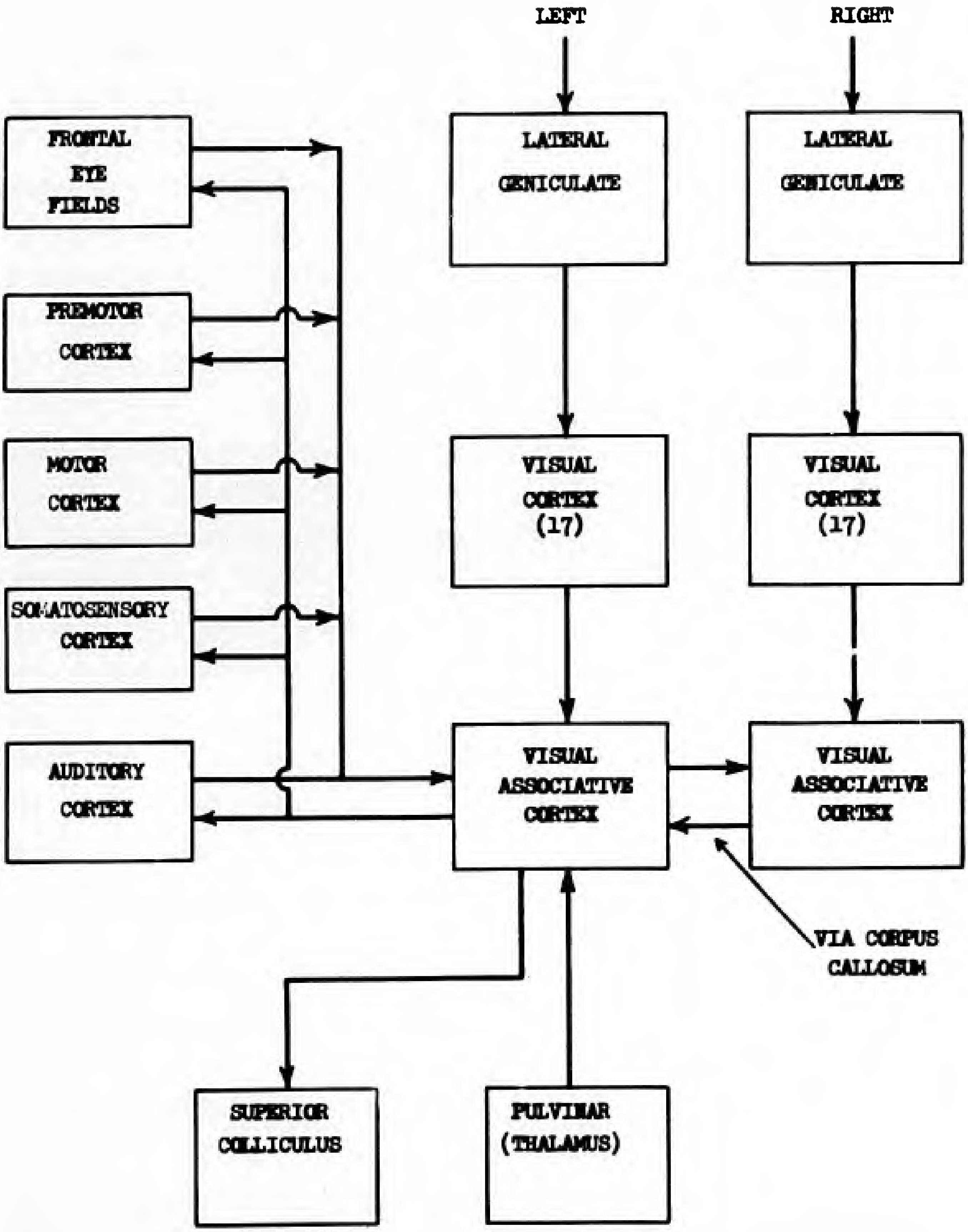


Fig. 13. Higher visual data processing and integration with motor and other sensory systems.

Actually there are several related mechanisms which, in concert, achieve this goal: mechanisms of fixation, mechanisms of focussing the image of the object upon the retina, and mechanisms of binocular fusion (or suppression of the image from one eye when fusion is not possible). In this section we shall be concerned with mechanisms of fixation.

In man, the neural circuits regulating fixation involve two modes of control: a "course" or "voluntary" control by means of which a particular object of the visual field is selected for primary consideration; and a "fine" or "involuntary" control whereby an object previously selected is "locked" into fixation regardless of movement of the object or shifts of position of the observer's head.

The "coarse" control initiates fixation movements from a small region of the frontal cortex located in front of the motor cortex. Control is contralateral, i.e., activity in the left frontal eye field produces movement of both eyes to the right, and vice versa.

The "fine" control locks the gaze upon the fixation object by means of a complex neural network, the decision-making component of which is apparently located in area 19, a cortical area surrounding area 18. If this area is destroyed bilaterally the individual loses the ability to lock his gaze upon a particular visual object.

Since both coarse and fine controls for image fixation require eye movements, it is appropriate at this time to consider the neural mechanisms involved.

Rotation of the eyeballs may occur in three orthogonal planes or combinations thereof, as illustrated in Fig. 14. Rotation in each plane is under the control of a particular pair of extraocular muscles. In the horizontal plane, rotation is produced by combined action of the lateral and medial rectus muscles. In one vertical plane parallel to the anterior-posterior axis of the head, rotation is produced by the superior and the inferior rectus muscles. This plane is called the sagittal plane. In another vertical plane, perpendicular to the sagittal plane, rotation is produced by the superior and inferior oblique muscles.

The cell bodies of the motor neurons which control eyeball rotations are located in the brain stem, and their axons to the eyeball muscles are carried in three "cables," the oculomotor, trochlear, and abducens nerves.

These motor nuclei receive inputs from a variety of sources, of which three are of major importance.

The first of these is from the vestibular nuclei of the brain stem. These nuclei receive signals from receptors fo the "inner ear" or labyrinth, especially from the semicircular canals, which detect rotations of the head. Interestingly, the semicircular canals also form an orthogonal system, and motion in each plane of rotation controls, by reflex, eye movements in the corresponding plane. This stabilizes gaze so as to

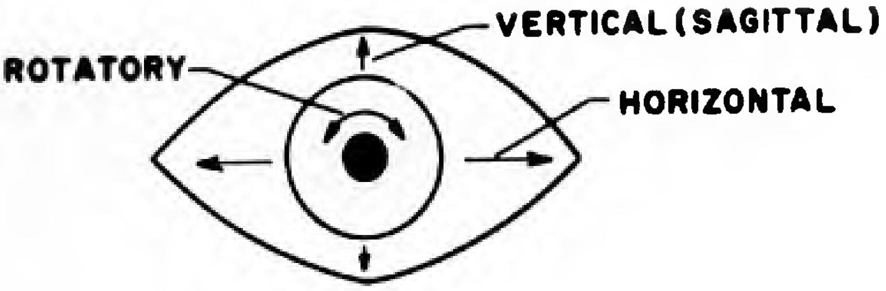


Fig. 14. Orthogonal rotations of the eyeball. (Note: the axes of rotation are not exactly orthogonal. The axes of sagittal and rotatory movements are somewhat "tilted" from the horizontal.)

maintain it constant regardless of small movements of the head. (If this movement exceeds a certain threshold, however, the direction of gaze may be quickly shifted to the center of the new field of vision -- unless this vestibular reflex is over-ridden by command from the motor cortex.)

The second major input to the eye muscle motor nuclei comes from the superior colliculus. This center in turn receives inputs from the optic nerve and also from areas 19 and 18 of the cerebral cortex. This apparently is the main channel for "fine" control of fixation, referred to above. A direct channel from areas 18 and 19, which bypasses the superior colliculus, has also been demonstrated.

The third major input to the eye muscle motor nuclei comes from the frontal eye fields. These fields are the command center for voluntary control of eye movements. Apparently the command channel is direct, bypassing the motor cortex (area 4).*

In addition to these input controls to the eye muscle motor nuclei, other channels play an important role in image fixation. These channels connect the frontal eye fields with areas 18 and 19 of the visual cortex. They apparently transmit information to these areas of the "command decision" of the target selected for fixation. Based on this command, the "fine" control of fixation locking gaze on target is exercised. The "cables" conveying this information from the frontal eye fields are the superior and inferior occipito-frontal fasciculi, and other long association bundles of the cerebral hemispheres.

This "command signal" from the frontal eye fields exercises an "overide" effect on reflex following movements stimulated by other, moving targets of the visual field. This is demonstrated by experiments in which the subject looks at a rotating optokinetic drum but focusses voluntarily beyond it. The following responses, ordinarily elicited in the absence of this voluntary focus, are at least partially inhibited by this experiment (Crosby, p. 486).

The mechanism of fixation on a stationary target involves three types of eye movements (Whitteridge, 1959). These are:

1. A continuous tremor with amplitude of 4 to 6 seconds at a frequency of 30 to 50 cps.
2. Occasional "flicks" of 5 to 60 minutes at irregular intervals.
3. A slow drift of about one minute of arc per second of time.

---

*Although eye movements can be produced by stimulation of the appropriate part of the motor cortex (area 4) destruction of this region does not lead to paralysis of voluntary control of eye movements. Destruction of the frontal eye fields, however, does produce such paralysis. (Crosby et al, p. 488)

The continuous tremor moves the detail of the visual image across the cones of the retina, reducing the adaptation that might otherwise occur, and also tending to excite the movement-sensitive retinal receptive fields. This process enchances visual discrimination and acuity.

If the image is stabilized (by viewing light which has been reflected by a contact lens, so that the image moves when the eye moves), visual detail seen rapidly decreases. Thus continuous tremor plays an important part in visual acuity.

The tremor also provides a "hunting" type of oscillation enabling gaze to be locked upon a target -- especially useful if the target moves.

The "flick" movements operate to correct for drift (Whitteridge, 1959).

If the target is moving, eyeball movements called "pursuit" movements occur. These are usually jerky ("step" mode of operation), an appropriate pursuit for the usual type of random movement of visual targets. However, if target movements are deterministic (purposeful) rather than stochastic, the pursuit mode may shift to one which minimizes tracking error. This is illustrated in Fig. 15, adapted from Stroud. Evidently neural computation detecting the law of movement of the tracked object is utilized to adjust the mode of pursuit.

Recent studies of eye fixation control from the standpoint of modern control system theory and analytical techniques have been reported by Fender and Nye (1961) and Dallos and Jones (1963).

Automatic Focussing Control

One of the differences between the human eye and a camera is that the eye possesses an automatic focussing control. Within certain limits, whenever the visual system fixates upon a particular object in the field of vision, the curvature of the lens is automatically adjusted to bring the image of the fixated object into focus on the retina.

This process, called accommodation, depends upon the mechanical properties of the lens of the eye. The lens of a child is relatively flexible and his range of accommodation is quite large. As an individual grows older, the lens of his eye becomes more and more rigid, until in old age practically no change in shape is possible under physiological conditions. Such a person no longer has the ability to accommodate, and his automatic focussing control is no longer effective.

The shape of the lens is changed by contraction of a tiny muscle inside the eyeball called the ciliary muscle. When this muscle contracts, tension on the elastic fibers suspending the lens is released, permitting the lens to become more spherical. Conversely when the ciliary muscle relaxes, the fibers suspending the lens are stretched and the lens becomes flatter.

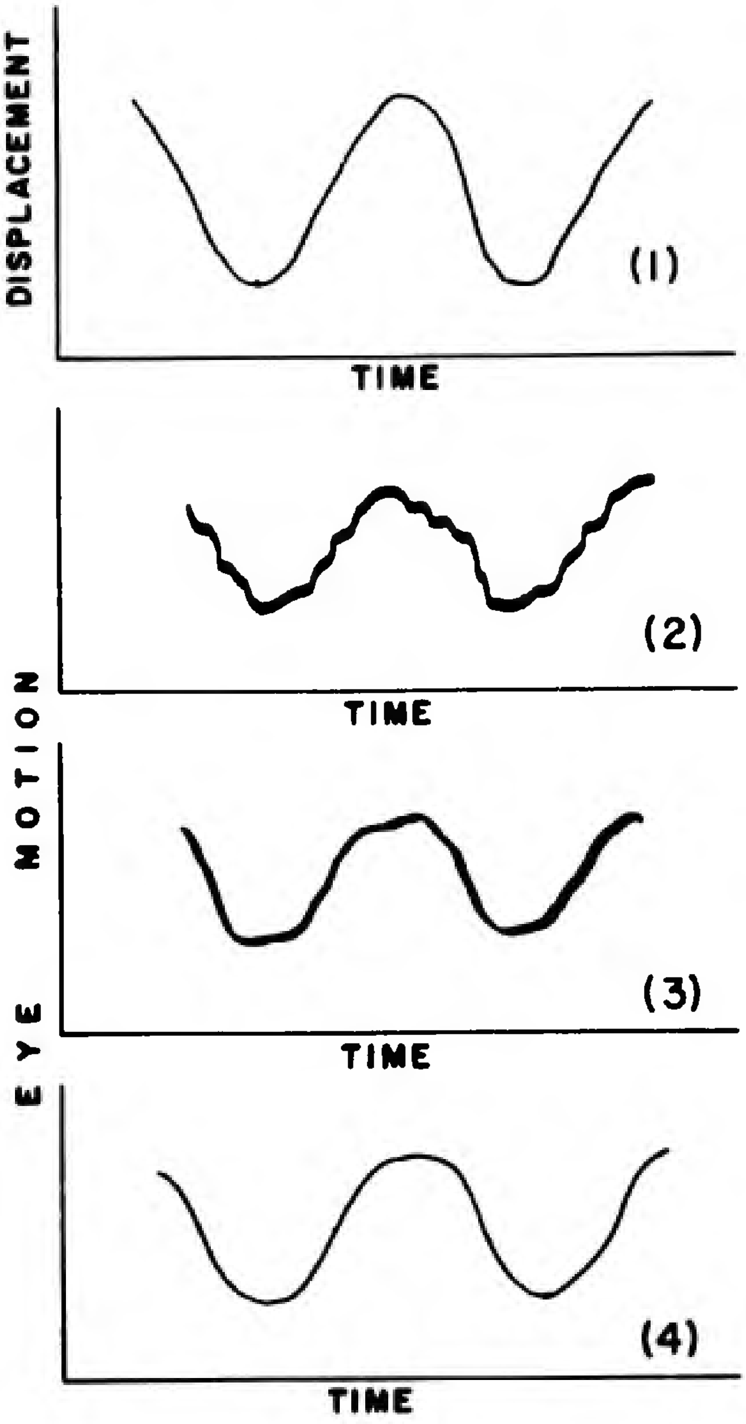


Fig. 15. Pursuit Mode. (1) Actual motion of the target. (2) First solution of tracking problem. (3) Second (velocity) solution of the tracking problem. (4) Third (acceleration and velocity) solution. (After Stroud).

The ciliary muscle is in turn controlled by parasympathetic nerve fibers originating in the ciliary ganglion, a tiny nerve center about a centimeter behind the eye, not itself included within the central nervous system. The ciliary ganglion in turn receives inputs from a nucleus in the mid-brain called the Edinger-Westphal nucleus.

There are two theories of automatic focussing control. One theory, advanced by Wilkinson (1927), is based on the fact that accommodation is always associated with convergence of the eyeballs. According to this theory, when a target is selected in the visual field, nerve signals from stretch receptors in the extra-ocular muscles are transmitted to the Edinger-Westphal nucleus bringing a concomitant change in focus.

The other, more generally accepted, view (Crosby et al.,p. 244) is that accommodation is under control of the superior colliculus. This center, as described above, receives inputs both from the retina and from areas 18 and 19 of the cerebral cortex, the latter the main channel for "fine" control. According to this theory, when neural signals from the retina indicate blur of the retinal image of the visual target, the superior colliculus generates commands to the Edinger-Westphal nucleus bringing about a change in accommodation. This is illustrated in Fig. 16.

It is evident that the "on" and "off" receptor fields of the retina are admirably suited for signalling degree of sharpness of contours of retinal images. An image in focus would evoke high-frequency discharges in the receptor fields stimulated by the contours of the image; a blurred image would evoke lower frequency discharges from a wider band of receptor fields. A mapping of blurred and focussed images may thus be transmitted to the superior colliculus. The neurons of this nucleus could easily be organized so as to compare the mapping of images with the fixation command signal from areas 18 and 19, and if the selected image is blurred, the nucleus could generate a command to adjust the degree of accommodation until optimum focus occurs.

An automatic focussing camera utilizing this principle would appear to be technologically feasible.

INTENSITY CONTROL

Adaptation

The sensitivity of the retina may vary over a remarkably large range -- from a response to a few quanta of light at the highest sensitivity level (in the dark) to a sensitivity one half-millionth as great (in strong light). This automatic sensitivity control is called adaptation.

Adaptation is a complex process. In the first place, adaptation to light follows a different time course from adaptation to dark, as shown in Fig. 17. Light adaptation is a much faster process than dark adaptation.

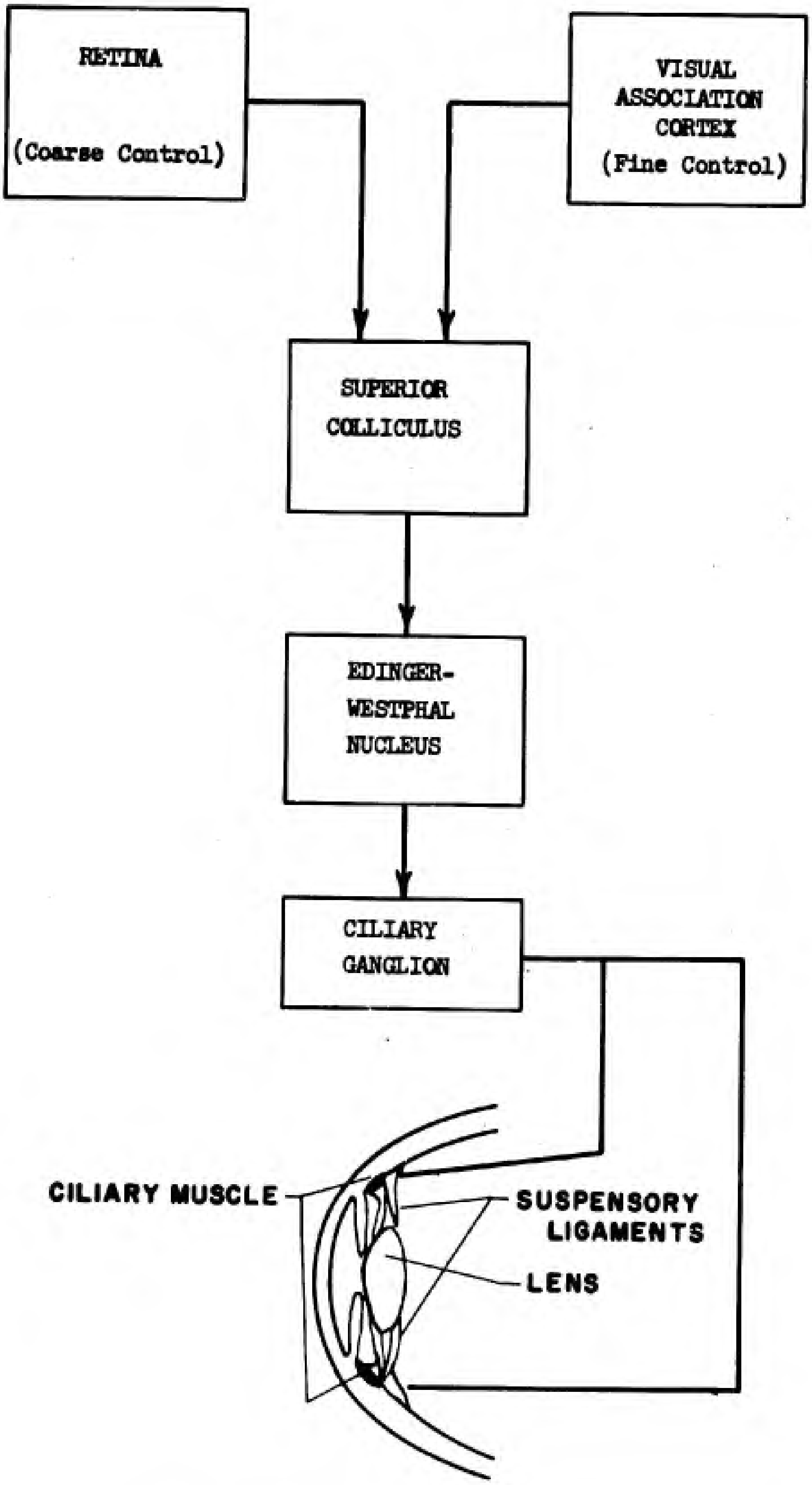


Fig. 16. Control circuit for accommodation.

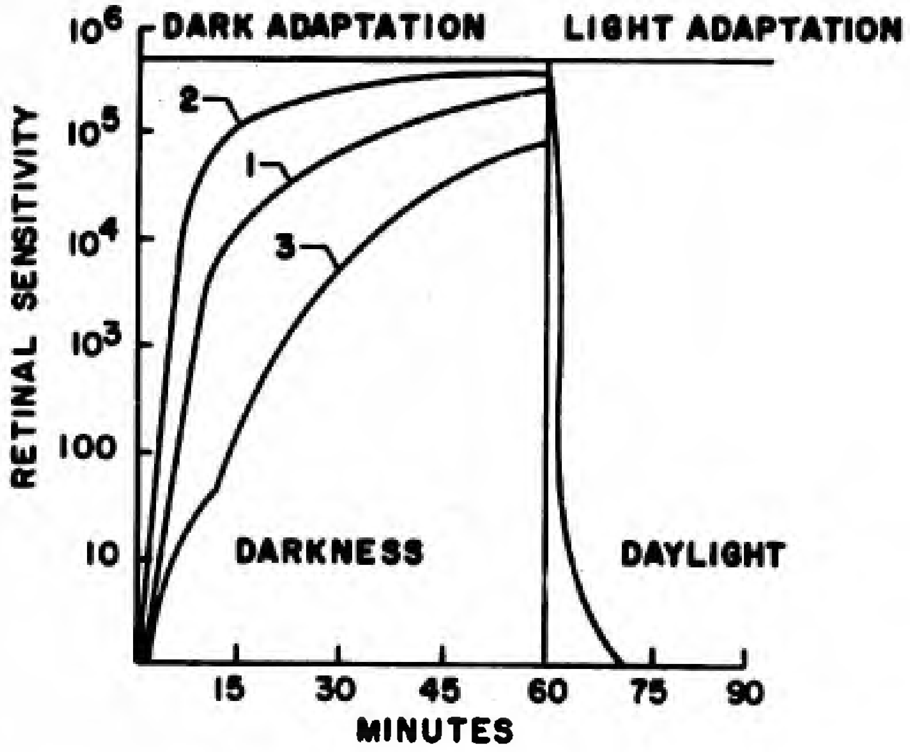


Fig. 17. Dark and light adaptation (after Guyton). Curve 1 represents dark adaptation after 20 minutes in bright light. Curve 2 represents dark adaptation after a few minutes in bright light. Curve 3 represents dark adaptation after several hours in bright light.

In the second place, dark adaptation is a composite process. The cones and the rods dark-adapt at different rates. Cone dark-adaptation occurs much more rapidly, achieving saturation in about 10 minutes. Rod dark-adaptation starts more slowly and does not reach saturation for an hour or more. Since the retinal channels for rod information transmission have a high degree of convergence, the rods at maximum dark adaptation are much more sensitive than are the cones.

The automatic sensitivity control performs the equivalent of a running time average on the average light intensity of the immediate past. From a bionic standpoint there is nothing new in this, aside from the relatively large range of adaptation involved, and the asymmetry of the process. This is made possible by the remarkable properties of the photopigments, which are capable of absorbing a relatively large proportion of incident light quanta.

Also important in this process, though usually overlooked, is the pigment epithelial layer of the retina, which also has a high capacity for absorbing incident light. Without this layer, light not absorbed by the photoreceptors would be reflected and scattered in the eyeball. Such a scattering would induce a greater degree of light adaptation, probably reducing visual acuity.

Classically, light and dark adaptation have been explained in terms of photochemical processes in the rods and cones, resulting in a decrease in photopigment in light adaptation and an increase in dark adaptation. Recent work by Lipetz has demonstrated the existence of another mechanism for light adaptation (which may account for its more rapid time course). Lipetz found that illumination of any portion of a receptive field produced light adaptation of the entire field. This phenomenon cannot be accounted for by the classical photochemical theory. Lipetz suggests that this process is probably the result of a spread of increased negativity of horizontal cells of the retina, producing an inhibitory effect on transmission of excitation from neighboring zones of a receptive field.

Pupil Aperture Control

The pupillary aperture may vary in diameter from about 1.5 mm to about 7 to 8 mm, corresponding to a range of pupillary area of about 25 to 1. Modification of pupillary aperture serves two functions: first, it limits the depth of focus in near vision, thereby reducing spherical aberration; and second, it modifies the amount of light entering the eye, thereby functioning, to some degree, as an adaptive mechanism supplementary to the dark- and light-adaptation systems discussed above.

If a beam of light is shone into one eye, the pupillary apertures of both eyes are reduced, although not in equal degree. This is the pupillary light reflex, and is one of the mechanisms by which the pupillary aperture may be controlled. Recently this control system has been extensively studied by Stark and his co-workers (1957, 1959) using servoanalytic techniques. A block diagram of this control system is given in Fig. 18. The neuroanatomical channels are shown in Fig. 19.

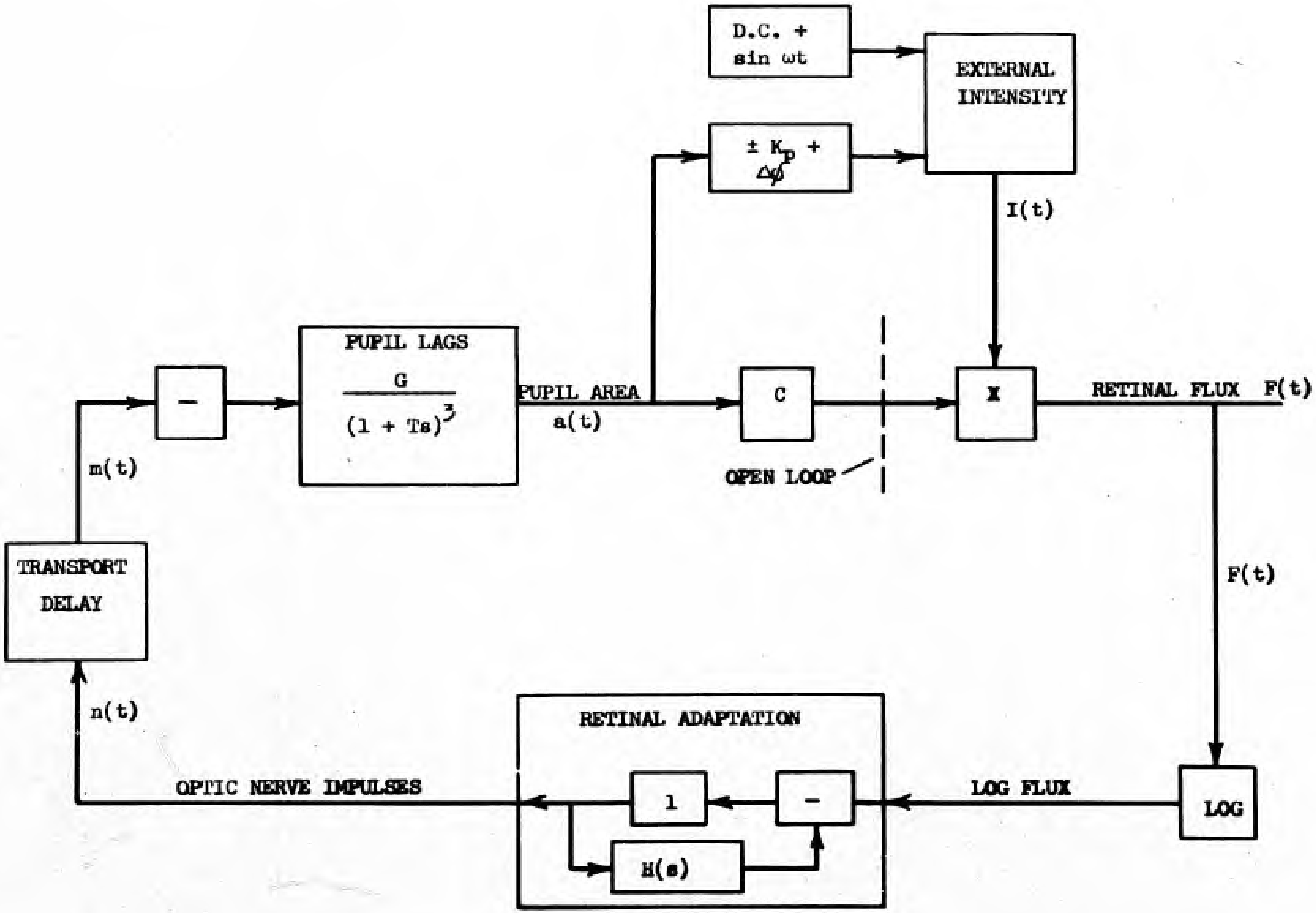


Fig. 18. Pupillary control system (after Stark).

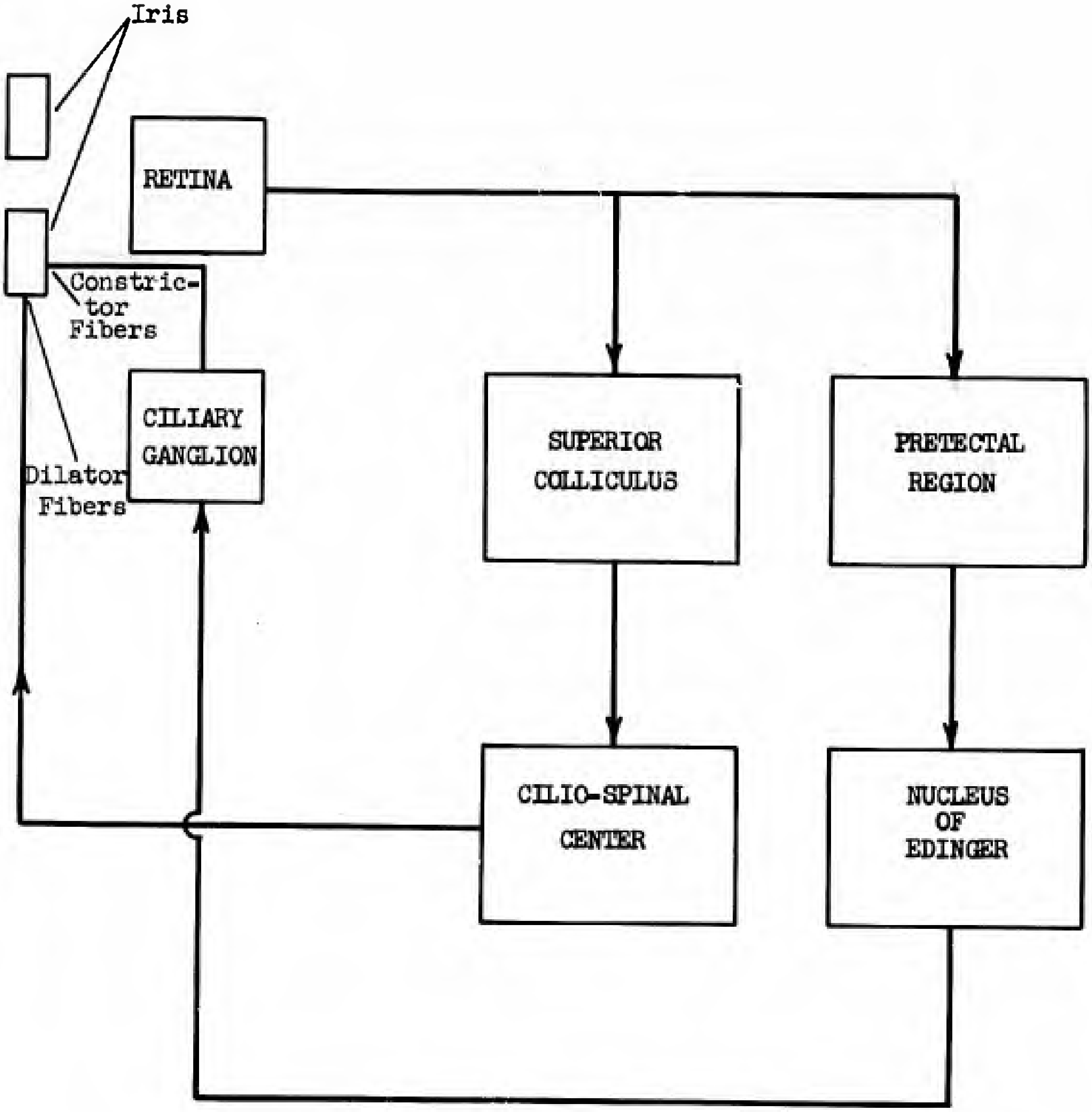


Fig. 19. Neuroanatomical channels of pupillary control system (various sources).

The pupillary aperture is also adjusted concomitantly with changes in fixation on visual targets. When the gaze is shifted from a distant object to a near object, the pupils constrict; and vice versa. Also associated with changes in fixation are changes in degree of convergence of gaze of the two eyeballs.

BINOCULAR CONTROL

Image Fusion

One of the most remarkable and least understood capabilities of the visual system is its ability to bring fusion of the neural mapping of a fixated visual target focussed upon the retinas of the two eyes.

Actually, the two processes -- fixation and image fusion -- are closely interrelated, and it is only for convenience of communication that we consider them separately. Image fixation, as previously described, is a process involving command selection of a visual target, automatic locking upon that target with respect to its movements in the visual space, and automatic focussing as it approaches or recedes from the observer. Coupled with this automatic focussing are changes in the convergence of gaze of the two eyes, a process essential for image fusion and important for depth perception.

In addition to changes in the degree of convergence of gaze (essential for fusion in the horizontal plane), the direction of gaze of the two eyes in the two other planes of rotation (involving vertical and torsional movements) must also be coordinated.

It is commonly stated that corresponding points of the two retinas are those which, when stimulated, give rise to a single sensation. Such a definition is essentially psychophysical, based on use of the observer as a null instrument; and while remarkably sensitive and reproducible measurements can be made, no real insight into mechanism is provided.

As previously noted, although neural channels from corresponding halves of the visual field go to each lateral geniculate nucleus, in the monkey (and, presumably, in man) there is no neural basis for comparing visual information at this level; the channels from the two eyes are kept separate until the primary visual cortex (area 17) is reached.

A neurophysiological definition of corresponding points is made possible by the work of Hubel and Wiesel (1959, 1962), as well as by the earlier work of Talbot and Marshall (1941). These workers have shown that single neurons of the visual cortex of the cat are influenced by receptive fields from the two eyes. There is a striking degree of correlation. Thus, for example, if the receptive field of the neuron in the ipsilateral eye is simple, responding to a moving slit with a particular orientation, it is usually the case that the receptive field of the neuron in the contralateral eye is also simple, and responds best to a moving slit with the same orientation.

We can, therefore, define corresponding receptive fields in the two retinas as those which, when stimulated by a given stimulus pattern, produce excitation of the same neuron in the cat visual cortex.

The neurophysiological mechanism of image fusion, then, consists of that system which controls the directions of gaze in the two eyes in such a way that the visual target is focussed upon corresponding receptive fields of the two retinas.

There are two distinct but coordinated mechanisms involved in convergent movements of the eyeballs. The first, accommodative convergence, functions as a part of the "fixation triad" -- accommodation of the lens, pupillary constriction, and convergence of gaze -- which occurs whenever the individual fixates upon a visual target in the near field of vision. The second, fusional convergence, occurs when the fixated target is not focussed upon corresponding receptive fields in the two retinas.

Both accommodative convergence and fusional convergence utilize the same brain stem control center for the ocular muscles involved (Fry, 1959); however, the cortical components of the control hierarchy involved appear to be distinct. Accommodative convergence is part of the fixation control system previously discussed. The cortical component for the control system for fusional convergence probably includes at least some of the neurons of the visual cortex having binocular receptive fields as described above. Other areas of the cortex may also be involved. A block diagram of the system is shown in Fig. 20.

Although our understanding of the fusion control system is still incomplete, the available evidence suggests a somewhat different mode of control than that of most engineering servomechanisms. According to Hubel and Wiesel, most visual cortical neurons having binocular receptive fields exhibit synergy rather than antagonism between the two fields. In other words, if, for example, a slit in a particular orientation in the receptive field of one eye excites the cortical neuron involved, the image in the contralateral receptive field also produces excitation; the two together sum. This suggests that, while an "error" signal resulting from retinal disparity of the two images may drive the convergent mechanism toward fusion, a "locking" signal may also be superimposed when fusion is achieved.

Closely related to visual fusion are the phenomena of binocular rivalry and image suppression. In certain visual situations fusion is physically impossible. Under these conditions a "rivalry" between the two images may occur, with now one image, now the other, being suppressed.

Frequently the image from one eye is permanently suppressed, in which case we say that the other eye is "dominant." Binocular rivalry or dominance are characteristic in the clinical condition called strabismus ("cross-eyedness"), where the fusion control system is apparently in an unstable state.

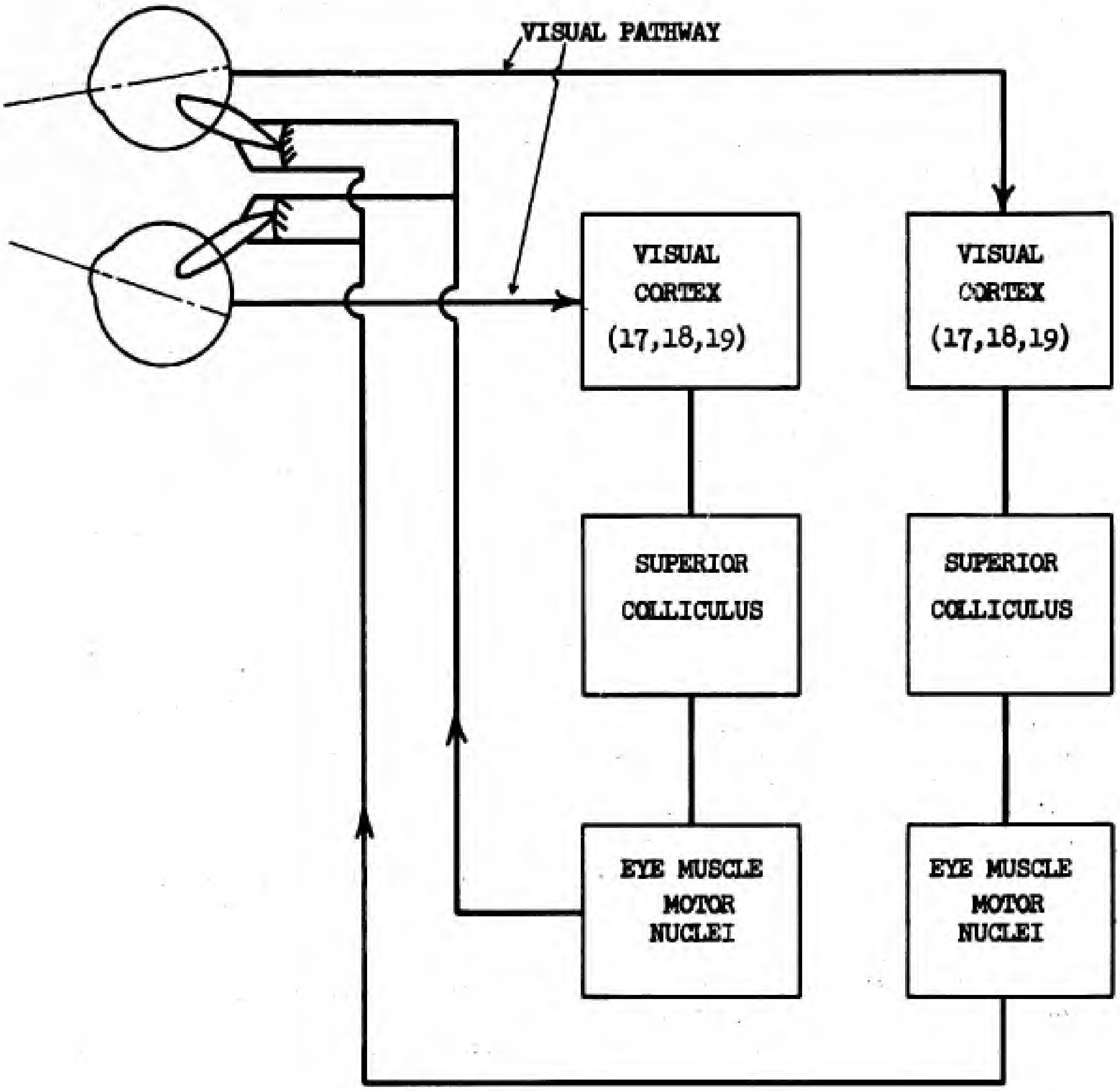


Fig. 20. Fusional convergence control system.

Depth Perception

Perception is far more than the neural equivalent of pattern recognition. Not only is a pattern to be identified as such, it is to be identified as a particular member of a class of objects. The class properties, accumulating through past experience, are available from storage for use in computations involving the objects. Depth perception is a particularly interesting kind of perception, which well illustrates this point.

The amount of monocular depth perception of which the visual system is capable is remarkable. This is achieved not by measurement of the distance of objects but by the use of a library of ingeneous programs for processing visual data. Apparently once visual patterns are recognized or identified they are subjected to additional processing, in which they are compared with neighboring objects and with stored data about the properties of the class of objects to which the given objects belong.

The most important programs employed are the following:

(a). Angular subtense -- the angular separation of the directions to the two ends of the object. This involves use of stored data about the "real" size of the objects of that class. Thus coins have a certain "known" size compared to wheels or other objects of similar shape.

(b). Geometrical perspective -- As an object recedes from the observer, the angular subtense decreases. If the object is relatively near, the rate at which angular subtense changes, per unit increase in distance, is relatively large. If the object is relatively distant, the rate of change of angular subtense, per unit increase in distance, is relatively small.

An object does not have to move for this program to be useful; for example, the way a set of railway tracks run together in the distance is an indication of how far they are away.

(c). Motion parallax -- If the head is moved, distant objects appear to move "with" the head; near objects appear to move "oppositely" to head movements. This is one of the most important programs for estimating distance.

(d). Overlap -- If object A is seen to cover a part of object B, object A is judged to be the nearer of the two.

(e). Shadowing -- If the shadow of object A is observed to fall on object B, object B is judged to be farther from the source of light. If the source of light can be located and its relative placement with respect to the two objects can be determined, the relative distance of the two objects from the observer can be judged.

Of course, the programs referred to above are not confined to monocular vision, and are ordinarily used in binocular vision. They merely do not require binocular vision. Stereopsis is the only mechanism in depth perception which is based on binocular vision.

Stereopsis is based on the fact that a near object A is focussed on a more temporal region of both retinas than a distant object B. This is best seen by referring to Fig. 21. In the left eye, the image A^1 is to the left of B^1; in the right eye, the reverse is true. On the other hand two adjacent objects equidistant from the observer, have the same relative positions in the two eyes, as shown in the figure.

Stereopsis not only helps in depth perception *per se* but adds a third dimension to visual space. Subjectively, it gives the impression of solidity. It is apparently the only mechanism of visual depth perception that has been employed technologically.

The neurophysiological basis for the processing of visual data involving depth perception is practically unknown. With the exception of stereopsis, the programs employed by the neural computer appear to be "logical" rather than "arithmetic"; they enable objects to be ordered according to relative distance, without providing quantitative measures of distance.

VISUAL ORIENTATION - STABILIZATION OF VISUAL SPACE

Following Luneberg (1947), we define visual space as the geometric manifold in which the apparent distance of any two sensed points is always proportional to the geometrical distance (as determined by the metric of the manifold) of the correlated points.

Visual space, as thus defined, is obviously different from the three-dimensional Euclidean space whose points are generated by intersections of the optical axes of the two eyes as they are directed in binocular vision. Visual space has a hyperbolic metric and is non-Euclidean. The reader is referred to Luneberg's excellent monograph for details.

It is apparent that visual space is stabilized, with reference to movements of the head, in a manner suggestive of the stabilization of tracking platforms on naval vessels. This is easily demonstrated by tilting the head. For small tilting movements, a compensatory rotation of the eyeballs may be observed. Even for large movements exceeding the range of torsional rotation of the eyeballs, however, visual space appears "stable" to the observer. Evidently very subtle and efficient mechanisms

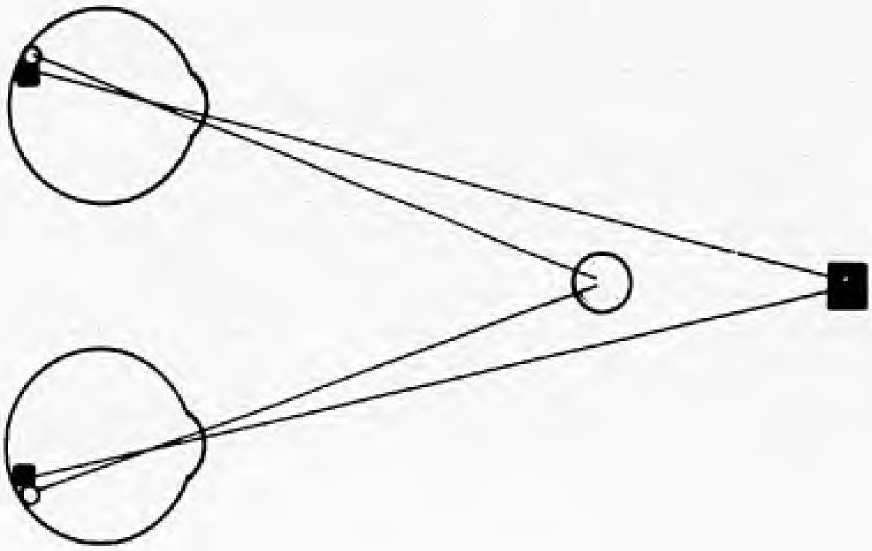


Fig. 21. Stereopsis. Image of distant object is on nasal side of image of near object on both retinas. If objects were equidistant but displaced laterally, their images would be similarly placed on both retinas.

operate to stabilize visual space in the face of a wide range of head movements. Indeed, the process of stabilization appears to function differently from the stabilization of tracking platforms.

As discussed above, one of the major inputs to the visual cortex (area 17) comes from the vestibular system, providing information about movements of the head in space. As has been shown by Groën and coworkers (1956), the semicircular canals operate according to the dynamics of a highly damped torsion pendulum. Together with the otolith organs, they provide precise information about the position and state of motion of the head. (Additional information about head position relative to the trunk is provided by proprioceptors of muscles of the neck, as well as joint receptors in the vertebral column of the neck.) This information is combined with visual data in area 17 to provide a stable coordinate system for visual space, regardless of head position.

There are conditions of motion in which the orientation of visual space does not coincide with the earth's gravitational field, as is normally the case. There are also conditions of motion in which vestibular information is strongly at variance with visual data; for example, after abrupt cessation of movement following a period of rotation in a "barber's chair." Of interest here is the ability of the central nervous system to "adapt" or "learn." As Groën has shown, the "cupolograms" of persons (e.g., stunt pilots) who have been subjected to a chronic high degree of vestibular stimulation are significantly less steep. Here, as in so many other instances, we are confronted with a "self-optimizing" capability of the central nervous system. How the brain does this we do not know.

In any event, visual space is apparently stabilized by a process of correcting the orientation of the coordinate system of visual space for movements of the head as signalled by vestibular data. Provision for optimizing the control of visual space orientation by some unknown means is also provided.

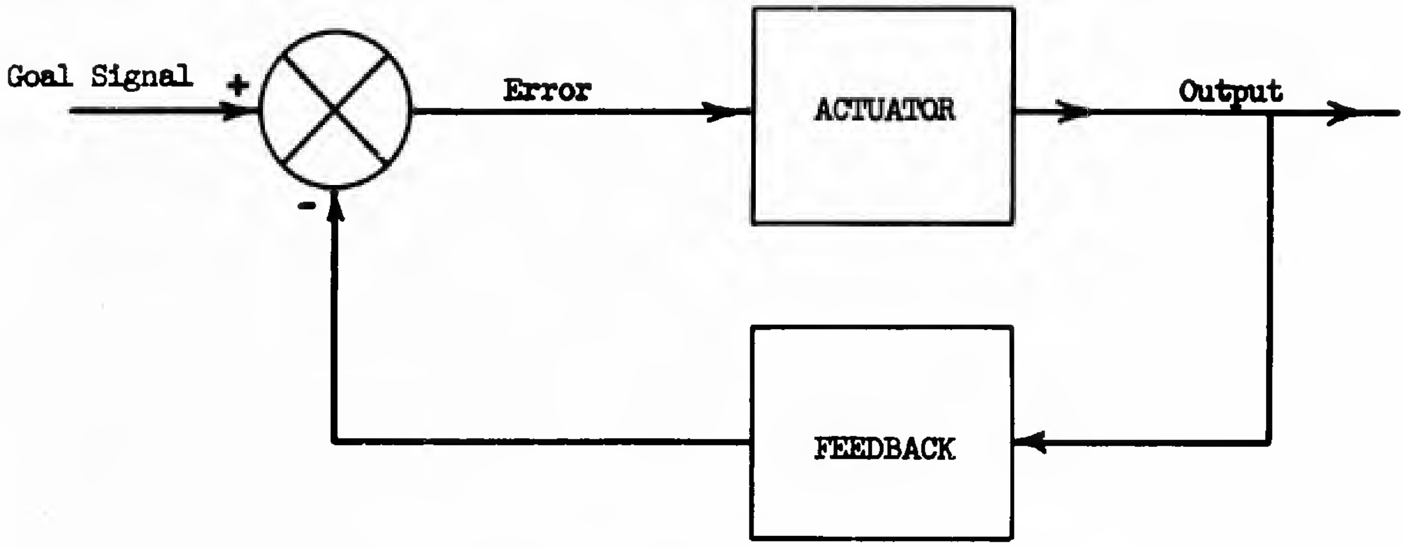
III. NEURAL CONTROL OF MOVEMENT

INTRODUCTION

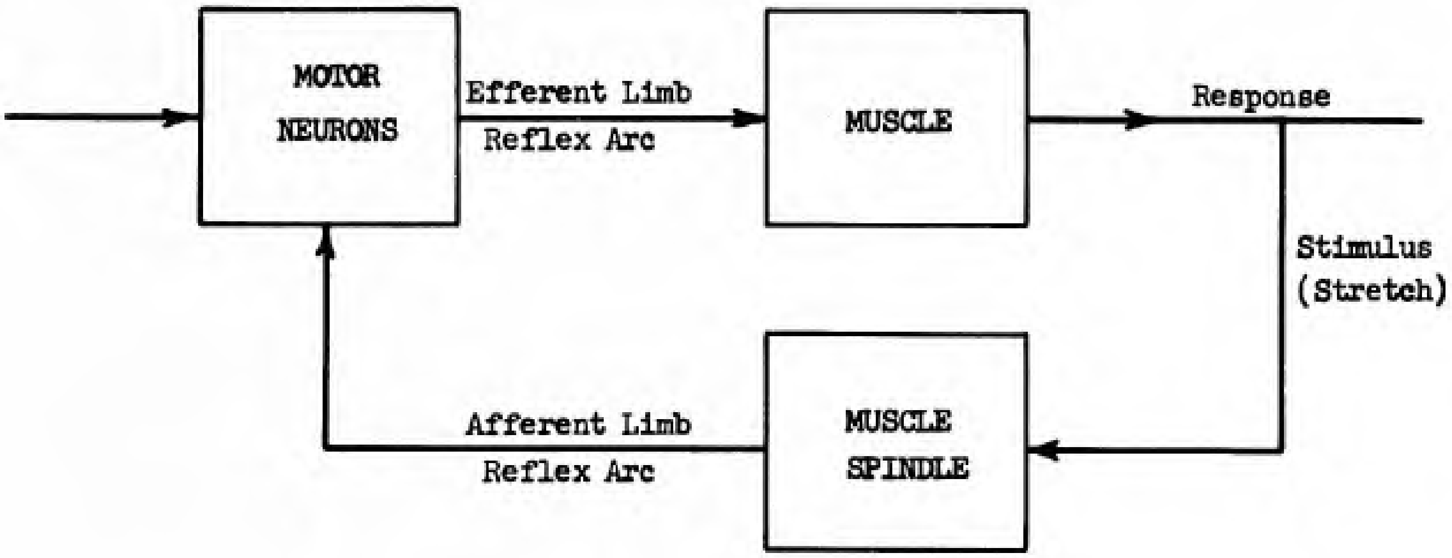
Human locomotion is extraordinarily versatile. In addition to such modes of movement as walking, running, climbing, and jumping, not to mention striking, kicking, and biting, there is an apparently unlimited number of highly specialized motor skills, ranging from piano playing to neurosurgery, from prestigitation to the operation of a lathe -- each skill involving coordination of involved sequences and combinations of unit motions. One special skill, the capacity to verbalize -- by speech or pen or typewriter -- is itself a motor skill of higher order. It is basic to a hierarchy of verbal skills involving the communication not only of simulated movement but the whole universe of simulations of which the brain is capable. Indeed, the simulation of verbal communication is itself a major mode of thinking, and may well be the way thinking gets its start. Certainly, such simulation sharpens our thinking processes and greatly extends their range.

The study of the neural control of movement has in the past been hampered by a number of stereotyped conceptual molds. Among these, two may be used as illustrative. The first is the tendency to identify movement with the motor portions of the nervous system. In reality all movements have sensory components indispensible to their effective performance. It may be convenient to analyze the control of movement from the special aspect of each of the principal motor components of the central nervous system, but in each case sensory processes are involved.

The second is the reflex formula according to which neural processes are interpreted in terms of stimulus and response. There is no question that reflexes exist, and that much has been learned by Pavlovian conditioning techniques as well as those of the behaviorist school of psychology. The problem here is the tendency to interpret all neural processes in terms of this formula and its elaborations. Other interpretations are also possible, and equally scientific. In recent years this has been well illustrated by the advent of cybernetics, and especially the theory of servomechanisms. According to the reflex formula, activity originated with a peripheral sensory stimulus and traverses simple or complicated reflex arcs to produce a response. A servomechanism, on the other hand, conceives activity as central in origin, in the form of a "goal" signal transmitted to a "mixer" or "comparator." The mixer output in turn produces muscular contraction (or glandular secretion) via the efferent limb of the reflex arc. Effector activity indirectly changes the environment of receptors, producing a "stimulus" (or change in previous degree of stimulation). This leads to altered activity along the afferent limb of the reflex arc -- the "feedback" path of the mixer (see Fig. 22). The mixer combines the feedback signal with the goal signal in such a way that the mixer output is an error signal -- it continues to drive the musculoskeletal apparatus until the actual position of the part coincides with the "goal" signal. When this occurs the error signal is zero and no further movement ensues. It should be noted that, with such an arrangement, the final position achieved is the same (for a given goal signal) regardless of the initial position of the part.



SERVOMECHANISM (TELEOLOGICAL MECHANISM)



MYOTATIC REFLEX

Fig. 22. The myotatic reflex as a teleological mechanism (servomechanism).

That the central nervous system operates in some such manner is indicated by recent experiments. Electrodes were first implanted under surgical anesthesia in the limb area of the motor cortex of cats (Delgado, 1952, 1959). After the animal recovered, it was stimulated electrically via the implanted electrodes. A "purposeful" movement ensued; for example, when one cortical point was stimulated the cat would slowly raise its left hindleg. The other limbs and the body during the course of the movement, adapted themselves so that posture was maintained. Of particular significance is the fact that the final position of the limb was the same regardless of its initial position.

When we come to examine the detailed mechanism by which this is achieved, however, we encounter some surprises; the animal servomechanism appears to employ a different scheme of organization to achieve its effects. This will be discussed further below.

It is also worth noting at this point that there is another intriguing difference between nervous systems and their technological counterparts, with respect to control to movement. Servomechanisms to produce movement in response to goal commands have been developed to a remarkable degree by engineers, and in recent years adaptive and self-optimizing systems of considerable sophistication have appeared. However, to the author's knowledge at least, in all such systems the "goal" or "command" comes from outside the servomechanism -- ultimately from a human being.

The central nervous system has an additional capability: it can generate its own goals. It is, in other words, self-motivating. How this is done remains obscure, although information is accumulating with recent developments in the use of chronically implanted electrodes.

From a bionic standpoint this suggests the prospect of development of teleogenetic systems -- systems capable of generating their own goals. Such systems would exhibit "purposive" behavior to a higher degree of approximation than even adaptive or self-optimizing servomechanisms. One might expect hardware having teleogenetic capability to possess a high order of versatility. A sketch of a theory of teleogenetic systems is included at the end of this chapter.

In the following sections the major known details of neural control of movement will be described. The organization of neuromuscular control, common to various modes of operation of the overall system will first be considered. Next, the main channel of control, the cortical command channel, will be discussed. Since any movement, no matter how simple, involves the coordinated excitation and inhibition of a variety of channels besides the "main command channel," the cerebellar coordinating system will then be presented. Finally, the stabilization of all these servomechanisms under remarkably broad variations in mode of operation and condition of load, chiefly by the so-called "extrapyramidal" system, will be described.

NEUROMUSCULAR CONTROL

The musculoskeletal apparatus is an elaborate system of joints and levers together with self-contained power units, the muscles, so organized as to enable production of an enormous variety of rotations* of restricted range about joint pivots. Characteristically, the system converts rectilinear movement of the power units into limited rotatory movements, in contrast to some mechanical engineering systems. The net effect of muscle action is to generate a couple, whose components act along the line of contraction of the muscle and along a parallel line opposite in sense through the joint pivot.

Muscles generally act in pairs, one producing a rotation, the other (antagonist) producing a counter rotation. Thus, for example, the biceps produces a flexion, the triceps an extension, of the forearm. The appropriate biomechanical unit would therefore appear to be all muscles associated with rotation of a link** about a given axis. For rotation in one sense to occur, with minimum energy expenditure, there must exist not only contraction of one muscle (or muscle group) but also simultaneous relaxation of the antagonist. This imposes a basic requirement upon the design of the neural networks controlling movement.

As might be expected, the fulfillment of this requirement is imbedded into the functional organization of the nervous system. This is called the Principle of Reciprocal Innervation. Thus, for example, if the stretch reflex associated with the quadriceps femoris of the front of the thigh is stimulated, resulting in contraction of this muscle, there occurs simultaneously an inhibition of the motoneurons innervating the hamstring muscle group.

For our purposes, we shall define a simple biomechanical control unit as the set of muscles which produce rotation (in either sense) of a link about a given axis, together with the neural networks primarily involved in control of this motion. (Some muscle groups power motion about several joints, as for example those producing finger movement or torsion of the trunk. Where this occurs, we shall speak of a compound biomechanical control unit.)

Although the field of biomechanics is relatively old and some excellent work has been done, (see, for example, Elftman, 1944; Steindler, 1955; Evans, 1961) from a biophysical or bionic standpoint surprisingly little has been done on the kinematics and kinetics of body movement, and the field of biomechanical control systems has been barely touched. What is presented here is therefore mostly descriptive in character.

A muscle is composed of a number of units, called fibers, which may be organized in various arrangements, as shown in Fig. 23. In general they are parallel or pennate in organization.

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*A small degree of translation may be produced.

**A link is defined as the distance between two axes (or axodes) of rotation.

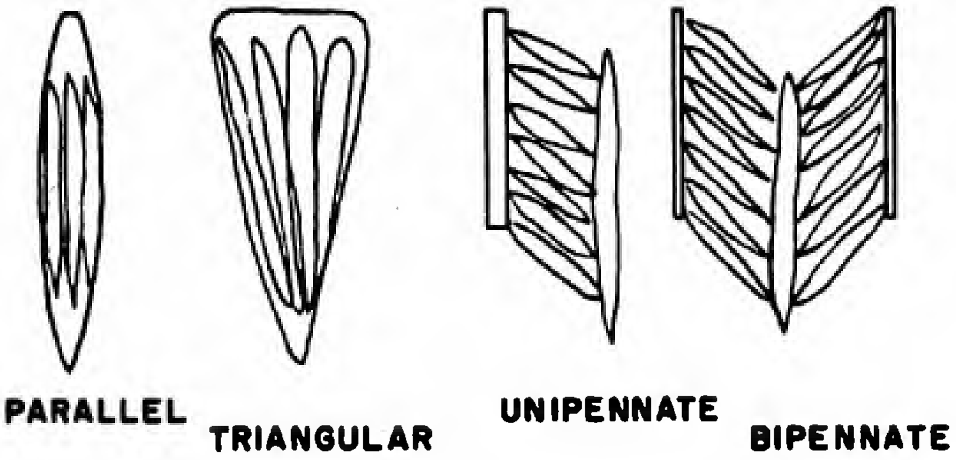

Fig. 23. Types of muscle organization.

Each motoneuron (whose cell body is located in the ventral horn of the grey matter of the spinal cord) sends branches to a number of muscle fibers -- from about 10 to 3000 depending on the muscle. A nerve impulse issuing from a single motoneuron thus brings about contraction of a number of fibers in a given muscle. The actual sequence of events is: nerve impulse, release of acetyl choline at nerve endings, depolarization of motor end plate of muscle producing the (nonpropagating) end plate potential, propagation of the muscle action potential away from the end plate, and, finally, the release of a brief burst of energy to produce a muscle twitch.

The muscle fibers innervated by each motoneuron thus twitch together. A smooth movement is achieved by the asynchronous firing of various motor units. This implies that the barrage of input activity to the motoneurons innervating a given muscle must be organized in such a way as to ensure temporal dispersion of firing times.

A simple biomechanical control unit consists of at least the following components:

(1) Two links together with an axis (or axode) of rotation.

(2) Two antagonistic muscles or muscle groups.

(3) The set of primary (α) motoneurons innervating each muscle.

(4) A region of the primary motor cortex (area 4), including the efferent axons which directly or indirectly synapse with the α motoneurons.

(5) Interneurons of the spinal cord which receive corticospinal or reflex inputs and synapse with the α motoneurons.

(6) The annulospiral endings of the muscle spindle together with the associated bipolar dorsal root neurons. These receptors sense displacement and velocity of muscle fibers.

(7) The γ motoneurons (fusimotor neurons) which innervate the intrafusal fibers of the muscle spindle (controlling "spindle bias").

(8) The Golgi tendon organs together with the associated bipolar dorsal root neurons. These receptors sense tension (passive or active).

(9) Joint receptors which sense degree of rotation of the joint.

(10) The proprioceptive channel via the spinal cord, brain stem, and posterolateral ventral nucleus of the thalamus

to the somatosensory cortex (areas 1, 2, and 3). A branch of this channel also goes to the cerebellum.

(11) "Association" channels interconnecting the somatosensory cortex with the motor cortex.

(12) The cortico-ponto-cerebellar control loop which connects the motor cortex to the cerebellum via the pons, with a feedback from cerebellum to cortex via the thalamus.

It should be emphasized that the definition here of the biomechanical control unit is tentative and based on existing evidence, which is still relatively meager. The components described definitely exist and are functionally interrelated in the manner described; but many details are lacking and other components and interrelations may exist which should be added to the system. Furthermore, we have omitted a number of systems, such as the extrapyramidal system, and the reticular system of the brain stem, which are quite important. Nevertheless it seems desirable to define and delineate a unit system which consists of components essential to the control of rotation of a link about a given axis, and the system thus defined (and illustrated in Fig. 24) seems to be the minimum required for this purpose.

How does this system operate?

While quantitative details are lacking and much remains unknown, we can tentatively describe its performance as follows. A "goal signal" is transmitted from the reticular system to the motor cortex. At the same time, a signal from the reticular system is delivered to the fusimotor neurons (γ motoneurons) of the spinal cord. This signal might be characterized as an "anticipation" or "altering" signal, which alters the bias on the muscle spindles in preparation for the movement to come. Other signals are probably also generated by the reticular system, but these need not be considered at the moment.

The motor cortex then generates a command signal which is delivered (directly or indirectly, via internuncial pools) to the bank of α motoneurons in the brain stem or spinal cord. A signal is also delivered via the cortico-ponto-cerebellar system to the cerebellum. Other signals are probably also generated, but these will be ignored in this somewhat oversimplified scheme.

The bank of alpha motoneurons, in response to the command signal from the motor cortex, generates signals to the muscle fibers they innervate, producing a set of asynchronous twitches which sum to produce a relatively smooth contraction of the muscle or muscle group. Simultaneously, the α motoneurons innervating the antagonist muscle or muscle group are inhibited. As a result, a rotation of a link about an axis through a joint is produced. The angle of rotation depends upon the tension developed by the muscle, the load on the link, and the "counter-tension" (passive or active) present in the antagonist muscle or muscle group.

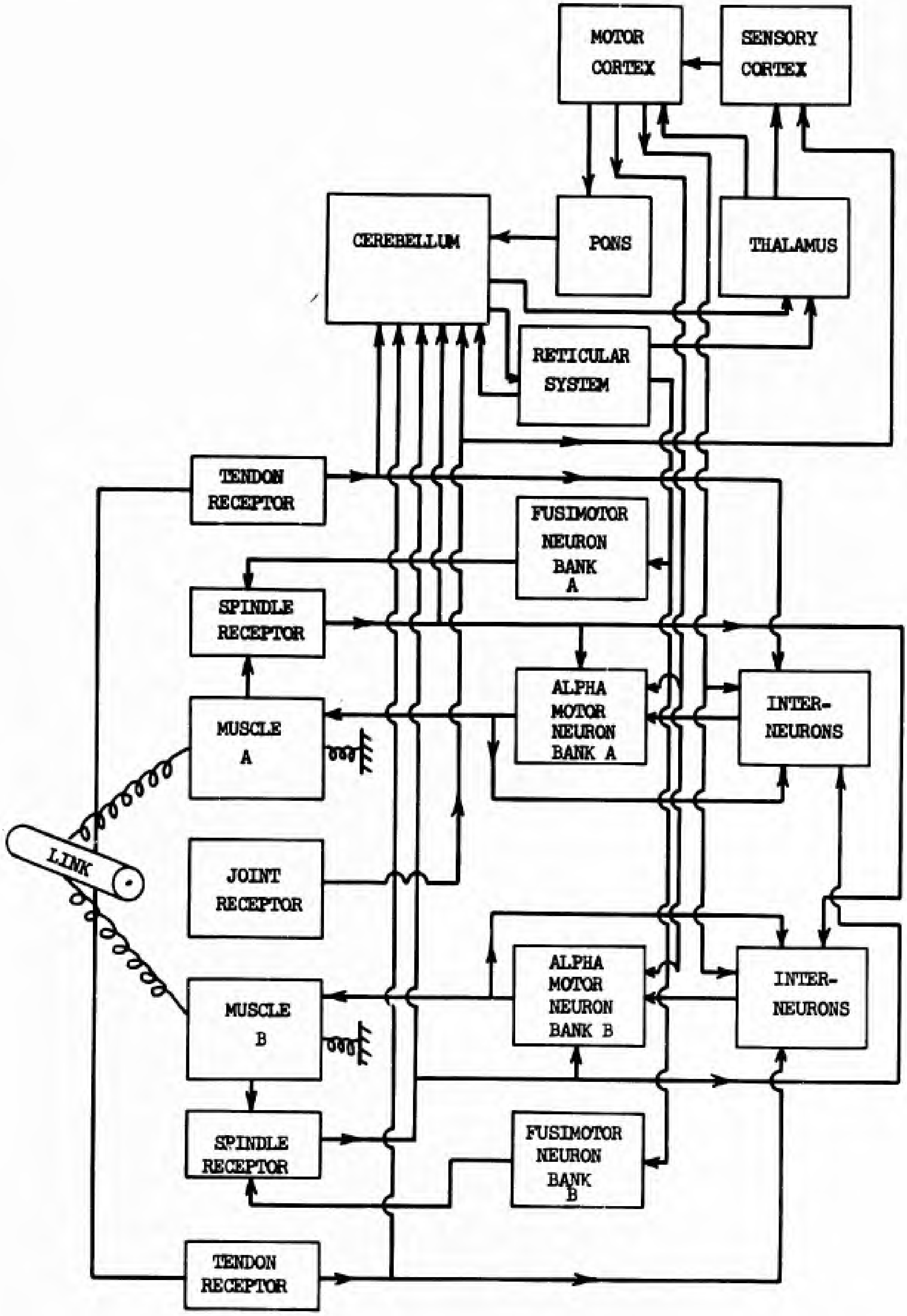

Fig. 24. Biomechanical control unit.

As rotation proceeds, several feedback loops may be "activated." The first, the familiar myotatic reflex, originates in the annulospiral nerve endings in the muscle spindle. These are stimulated by stretch of the spindle, reflecting stretch of the muscle as a whole. The frequency of nerve impulses produced for a given extension also depends upon the activity in the γ motoneurons innervating the spindle. Contraction of the muscle thus reduces the previous degree of activity of the spindle afferents. Conversely, as the antagonist muscle or muscle group is extended, the degree of activity of spindle afferents is increased. Activity in the spindle afferents, transmitted into the spinal cord, tends to produce reflex contraction in the muscle of origin, via a monosynaptic reflex arc, and facilitation and inhibition of α motoneurons innervating synergists and antagonists, respectively.

A second feedback loop is the inverse myotatic reflex. The receptors for this reflex are the Golgi tendon organs, located in the muscle tendon. These are not under γ efferent control. They respond only to extension. Since they are in series with the contractile elements, in contrast to the muscle spindles which are "in parallel," the Golgi tendon organs are stimulated both when the muscle contracts and when it is passively extended. The threshold of these receptors, however, is higher than that of the spindles. Activity originating in the Golgi tendon organs tends to produce an inhibition of the α motoneurons of the corresponding muscle.

A third feedback loop is that of collaterals of the α motoneurons These branch within the spinal cord and, probably via internuncial neurons, tend to inhibit the activity of neighboring α motoneurons. The relative importance of this feedback loop is still not clear.

These feedback loops are all relatively short. The proprioceptive afferents from muscle spindles and Golgi tendon organs not only synapse (directly or via internuncial neurons) with α motoneurons of the spinal cord; they also ascend in the posterior columns of the spinal cord into the brain stem. The ultimate destination of this channel is the cerebellum. In addition, afferent fibers originating in joint receptors transmit signals indicating joint rotation to the cerebellum. The cerebellum thus receives both command signals from the motor cortex and feedback signals from proprioceptors. Strategically, it is well situated to perform operations of comparison and coordination. That it does perform some such role is indicated by the effects of cerebellar damage or removal. One such effect is "volitional tremor." The patient at rest exhibits no tremor, but if a voluntary action is undertaken, a tremor appears, especially pronounced near the "terminus" of the movement.

Such a tremor, of course, is not produced by the cerebellum, but is an expression of inadequate performance of other neural networks in the absence of the cerebellum. The fifth feedback loop may be involved here. This consists of a proprioceptive channel from joint receptors to the somesthetic cortex, which in turn is closely interrelated with the motor cortex. According to Mountcastle (1957, 1959), joint receptors are the only proprioceptors with representation in the somesthetic cortex.

Finally, in addition to its feedback channel to the motor cortex, the cerebellum exerts a major part of its control over muscular movement via an output channel to the reticular system. This produces a pattern of facilitation and inhibition of α motoneuron activity via γ efferent modulation of muscle spindle bias.

This completes our scheme of a biomechanical control unit. Even though it is admittedly oversimplified, it is a rather complicated scheme. Nevertheless, it appears to be the minimal network essential for human locomotion, even of the simplest kind. The remarkable variety of human locomotor activities may be regarded as the result of coordinated combinations of activities of biomechanical motor units. Bearing this scheme in mind, we can now examine its various features in more detail.

THE CORTICOSPINAL COMMAND CHANNEL

Commands for the control of voluntary movement are widely believed to originate in the percentral gyrus (motor cortex). The basic evidence for this is well known. Damage to the motor cortex or its efferent channels to the α motoneurons results in paralysis. Electrical stimulation of the motor cortex (in anesthetized animals, in awake animals with implanted electrodes, and in human beings with local anesthesia during brain surgery) produces movement in the opposite side of the body. Specific areas of the motor cortex produce movements of particular regions, so that it is possible to "map" the body according to its motor representation (Penfield and Rasmussen, 1958). The movements produced are usually simple rotations about joint axes, although occasionally more complex movements are produced.

The motor cortex, like other regions of the cerebral cortex, is organized into six layers, as illustrated in Fig. 25. The scheme presented there is a simplified diagram based largely on the classical analysis of Lorente de No (1949). Inputs to any cortical region are of three types: specific inputs, which originate in subcortical structures, principally the thalamus; associational and callosal inputs, which originate in other parts of the cerebral cortex; and nonspecific inputs, the origin of which is not known, but which are believed to originate in the nonspecific projection system of the thalamus (thalamic recticular system). Within the cortex is a large variety of internuncial neurons, which may be classified into neurons with descending axons, neurons with ascending axons, and neurons with horizontal axons. Outputs from the cortex are of two types: associational and callosal outputs, which go to other parts of the cortex of the same and opposite sides, and projection outputs, which go to subcortical structures.

The projection outputs from the motor cortex comprise two main channels: the corticospinal channel, and the cortico-ponto-cerebellar system. The corticospinal channel goes to the α motoneurons of the brain stem and spinal cord. Most of the fibers of this channel cross over in the medulla to the opposite side, but some fibers do not cross. It has been estimated that from about one-sixth to one-third of the approximately one million fibers in the pyramidal tract in the medulla originate in the motor cortex. Of these, a relatively small number, about 30,000, are believed to originate in the large pyramidal cells of the motor cortex.

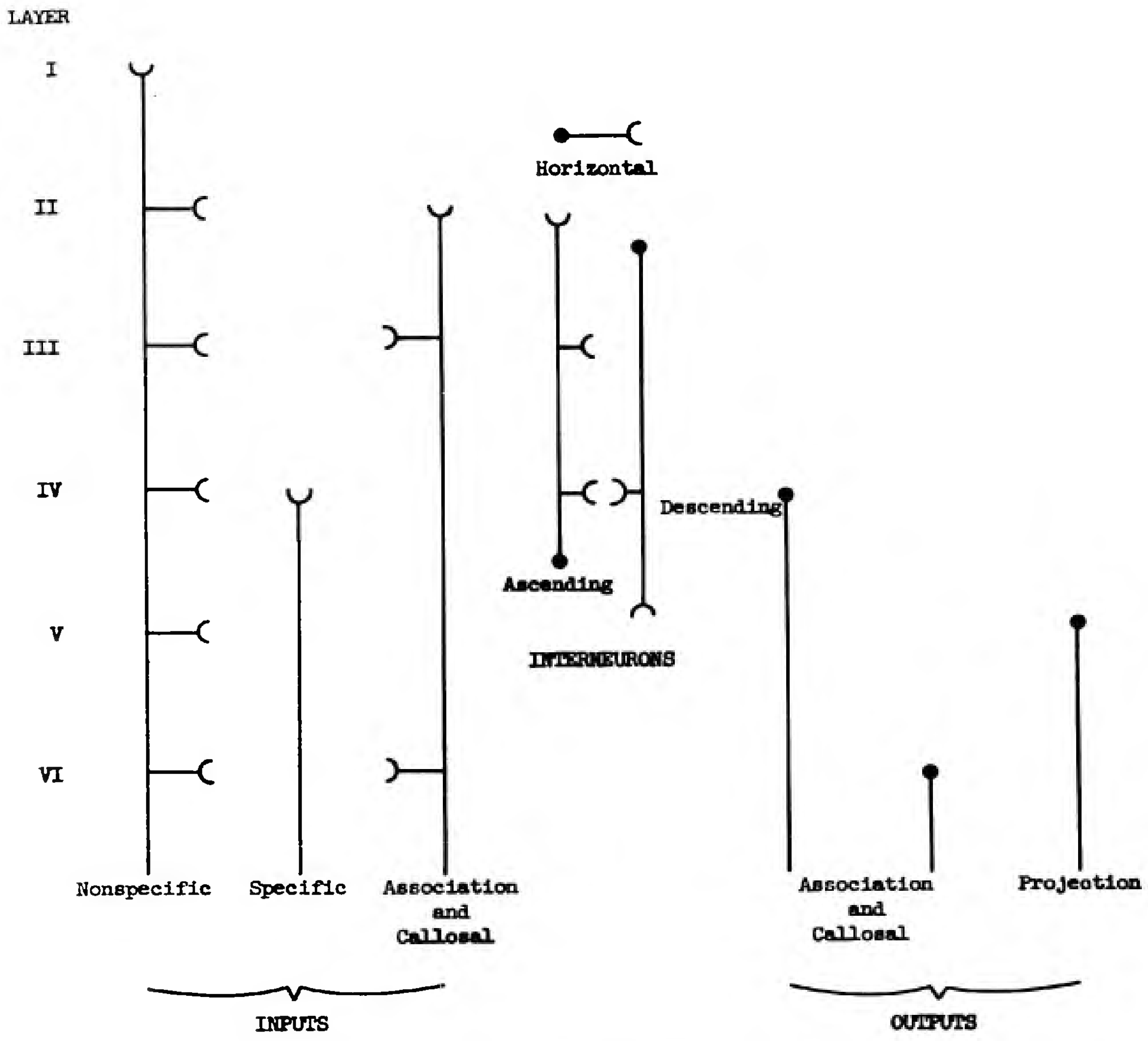

Fig. 25. Functional schematic of typical cerebral cortex (after Lorente de No). An organizational schematic.

The pyramidal* fibers not originating in the motor cortex arise primarily from the postcentral gyrus (somatosensory cortex), other parts of the parietal cortex, the temporal cortex, and the frontal cortex in front of the motor area. Kuypers (1960) has proposed that the fibers from the motor cortex go chiefly to the α motoneurons, either directly or via internuncial neurons in the cord or brain stem. Fibers from other cortical regions are believed to go to the sensory relay nuclei in the cord and brain stem, providing a neuroanatomical basis for cortical regulation of somatosensory inputs.

The cortico-ponto-cerebellar system provides a channel connecting the motor cortex with the cerebellum via relay nuclei in the pons. Neurograms traversing this channel are processed in the cerebellum together with signals from proprioceptors and other sense organs, eventually producing outputs which are fed back to the motor cortex via a channel through the red nucleus in the brain stem and other nucleus in the thalamus. Damage to this pathway results in the "volitional tremor" referred to above.

These two outputs from the motor cortex are not its only ones. Others have been described which go to the thalamus, the basal ganglia, and other subcortical structures (Crosby et al., p. 489). Conversely, ascending fibers from the spinal cord to the motor cortex which course in the pyramidal tract have been described.

As mentioned above, electrical stimulation of the motor cortex evokes simple rotations about joint axes. Microelectrode studies have shown that in order for movement to occur, the output neurons of the motor cortex must fire bursts of impulses; a single volley is not sufficient in itself (Phillips, 1956). Similarly, repetitive stimulation of the medullary pyramids produces movement, while a single volley does not (Adrian and Moruzzi, 1939).

The spinal mechanism for the transmission of cortical commands to α motoneurons has been carefully analyzed by Lloyd in the cat (1941). He found that there were few, if any, direct synaptic connections between the corticospinal tract and the α motoneurons. Rather, corticospinal activity was found to excite internuncial neurons in the spinal cord, which in turn produced a facilitatory effect upon the α motoneurons. His findings were corroborated by anatomical evidence.

Bernhard and co-workers (1945) investigated the spinal mechanisms for the transmission of cortical commands to α motoneurons in the monkey. They found that, in addition to the internuncial mechanism described by Lloyd, there exists a direct (monosynaptic) connection between the corticospinal channel and the α motoneurons. They referred to this channel as the corticomotoneuronal system. Repetitive firing of the corticospinal neurons was required before the monosynaptic response of this system could be elicited. The first volley of a train elicited a delayed response of the α motoneurons, evidently mediated via internuncials, and a state of facilitation was induced by subsequent volleys of the train. When this state of facilitation reached

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*The term pyramidal tract is derived from the pyramidal shape of the tract in the medulla, not from the "pyramidal" cells of the motor cortex.

a certain level, a monosynaptic response of the α motoneurons was produced with each subsequent volley of the train. After the train ended, internuncial activity continued for a gradually decaying "after-discharge."

Although the corticospinal channel is of major importance for voluntary movement, other channels are also important. Mention has been made of the fact that, in intact animals with implanted electrodes, stimulation of a particular region of the motor cortex produces a movement which proceeds to the same terminal position regardless of the initial position (Ward, 1950; Delgado, 1959). Stimulating a different cortical point produced movement to a different terminal position. The same phenomenon was observed when the underlying white matter was stimulated (Ward, 1950), even when the overlying motor cortex was removed (Cure and Rasmussen, 1954). Evidently a subcortical mechanism is involved. We do not know what this mechanism is, but the cerebellum appears to be a likely candidate for the office.

THE CEREBELLAR COORDINATING SYSTEM

The cerebellum is a fascinating organ. Its cellular structure embodies an amazing elegance and precision of organization. The output cell of the cerebellar cortex -- the Purkinje cell -- is one of the most remarkable of all neurons. The functional significance of the elegant microscopic organization of the cerebellar cortex is obscure; but it exists, and it is tantalizing.

The overall function of the cerebellum may be briefly described as that of maintaining postural equilibrium and poise in movement, and coordinating sequences and combinations of motor acts. To do these things a data processing network of considerable complexity is required. For students of modes of control of multivariable systems, the cerebellum has much to offer as an object of study.

The anatomical nomenclature of the cerebellum is confusing and in many cases meaningless from a functional standpoint. We shall follow the simple scheme of Larsell (1947, 1951) and divide the cerebellum into three main parts: the flocculonodular node, a phylogenetically old part of the cerebellum concerned with vestibular integration; the anterior lobe, primarily the receiving station for proprioceptive signals; and the posterior lobe, which is primarily the receiving station for the cortico-ponto-cerebellar system.

The basic pattern of data flow is as follows. Input signals are transmitted to the cerebellar cortex, a three-layered structure. The output signals from the cortex -- transmitted exclusively via the axons of the Purkinje cells -- are conveyed to a number of nuclei in the depths of the cerebellum -- the cerebellar nuclei. From these nuclei, signals are then transmitted to their various destinations -- such as the vestibular nuclei of the brain stem, the reticular system, the red nucleus and thalamus along the feedback path to the motor cortex, etc.

We have mentioned three major inputs: vestibular, proprioceptive, and the cortico-ponto-cerebellar system. Electrophysiological studies (Snider and coworkers, 1944, 1951, 1952) have shown that the cerebellum also receives major sensory inputs from cutaneous, auditory, and visual sources. Representation is bilateral, as is also the case for proprioceptive signals.

Finally, the cerebellum receives major inputs from the reticular system of the brain stem.

As mentioned above, the outputs from the cerebellum originate in the cerebellar nuclei, which receive the outputs from the cerebellar cortex. There are four pairs of nuclei: the dentate, globose, emboliform, and fastigial nuclei. The first three have apparently similar functions; they project to the red nucleus and to the thalamus (ventrolateral nucleus), from whence signals are relayed to the motor cortex. This is the great feedback loop to the motor cortex, interruption of which leads to intention tremor. The red nucleus, which receives some fibers and collaterals from this feedback path, also projects to motor centers in the brain stem and spinal cord.

The fastigial nucleus transmits signals to the reticular system of the brain stem, and to the vestibular nuclei. Some fibers also go to oculomotor nuclei, regulating eye movements.

A block diagram of the input and output connections of the cerebellum is shown in Fig. 26.

Let us next consider the elegantly organized cerebellar cortex. This is a three-layered structure, the output of which consists entirely of the axons of the Purkinje cells. Since the entire organizational pattern of the cerebellar cortex is based primarily upon these cells, it is appropriate to begin with a consideration of this remarkable neuron.

The external surface of the cerebellum is shaped into a number of long, relatively narrow folia (Fig. 27). The Purkinje cell is shaped like a flattened tree, placed at right angles to the long axis of the folium. Thus, in a section cut parallel to the long axis of the folium, a Purkinje cell appears as a relatively thin line. In a section perpendicular to the long axis of the folium, the Purkinje cell appears as a cell with an extensively branched dendritic tree. Each Purkinje cell has about 40 mm of spiny branches, with a total of about 60,000 spines (Fox and Bernard, 1957). The axons project downward into the white matter of the cerebellum, ultimately to connect to the cerebellar nuclei. Before emerging from the cortex, most axons give off one or more collateral fibers which return to synapse with neighboring Purkinje cells.

The Purkinje cells are separated from each other by about 3 mm in the longitudinal direction of the folium, and about 0.3 mm in the transverse direction. It has been estimated that a square millimeter of the Purkinje layer contains more than 500 Purkinje cell bodies (Fox, 1962).

The Purkinje cells receive three major inputs: from granule cells, whose cell bodies are located in the granular layer of the cortex below the Purkinje cells; from basket cells, whose cell bodies are located in the molecular layer above the cell bodies of the Purkinje cells; and from climbing fibers, one of the two major inputs to the cerebellar cortex.

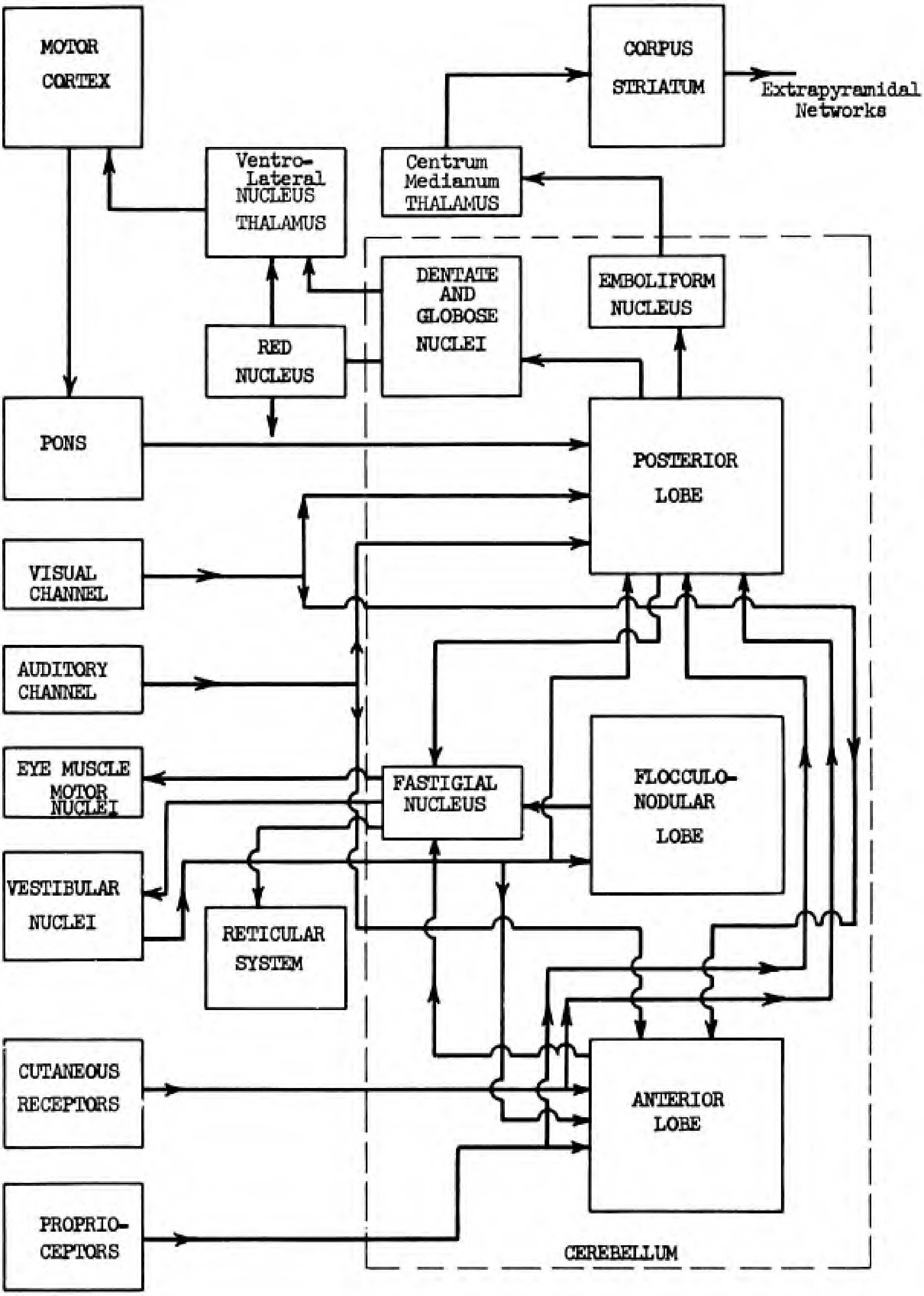

Fig. 26. Block diagram of cerebellar connections.

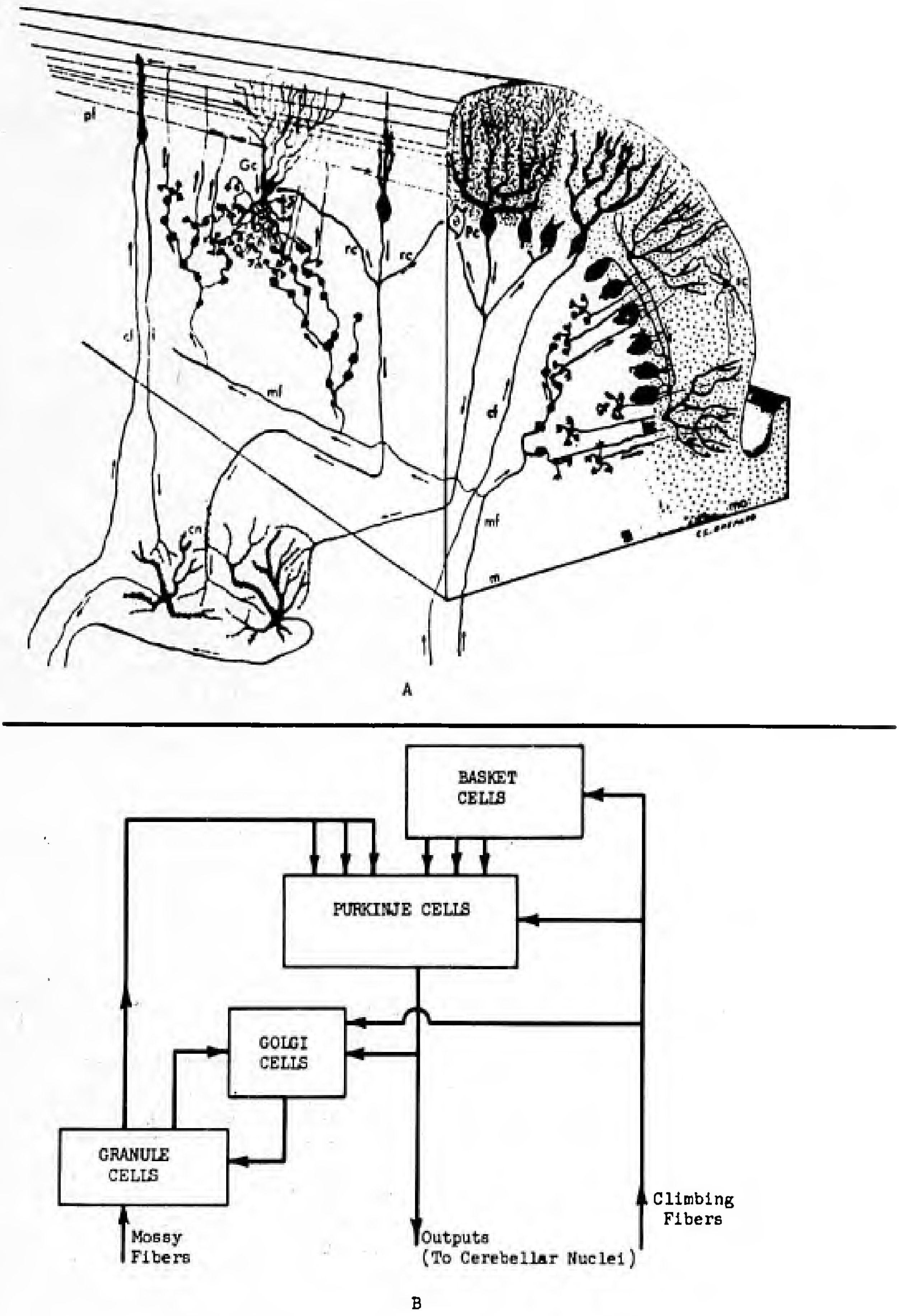

Fig. 27. A. Schematic view of a folium. bc -- basket cells; cf -- climbing fiber; Gc -- Golgi cell; gr -- granule cell; m -- medullary layer; mf -- mossy fiber; mo -- molecular layer; Pc -- Purkinje cell; pf -- parallel fiber; rc -- recurrent collateral; sc -- stellate cell. (After Fox).

B. Block diagram of cerebellar cortex.

The granule cells send their axons up into the molecular layer of the cortex. There they bifurcate into two main branches, which run parallel to the longitudinal axis of the folium (see Fig. 27). These branches synapse with the spiny terminals of the Purkinje cell dendrites; they are "strung along" the Purkinje cell dendrites much as telephone lines are strung along telephone poles -- except that there is considerable overlap from one cross-sectional zone to another; the Purkinje cells are not lined up like telephone poles. It has been extimated (Fox, 1962) that a parallel fiber 3 mm in length may form synapses with about 460 Purkinje cells.

The basket cells, whose cell bodies are located in the outer molecular layer above the Purkinje cells, provide an equally remarkable pattern of connection with the Purkinje cells. The axons from the basket cells branch in two directions: one parallel to the long axis of the folium, the other perpendicular to that axis (in the plane of a cross section of the folium). The transverse branches give off complicated "baskets" which "embrace" Purkinje cell bodies, terminating mostly upon the axonic cones. Each transverse branch contacts about 12 Purkinje cells. Each transverse branch in turn gives off longitudinal branches which similarly form baskets about 20 Purkinje cells, more or less. Thus, a given basket cell is connected to a rectilinear patch of about 12 by 20 Purkinje cells (approximately 240).

The climbing fibers (whose origin is unknown, other than that they originate outside the cerebellar cortex) ascend to the Purkinje cell layer whence they run in a climbing vine pattern forming axodendritic connections. The climbing fibers also make connections with basket and stellate cells as well as Golgi cells, as discussed below.

The Golgi cells have short axons which branch into dense plexuses. These cells are located in the granular layer, just below the Purkinje cells. Their dendrites reach upward into the molecular layer, where they ramify extensively. Their axonal terminals synapse with the claw-shaped dendrites of the granule cells. Their input synapses are with the climbing fibers, with the parallel branches of the axons of the granule cells, and with recurrent collaterals from the axons of the Purkinje cells. They are thus strategically situated to monitor both the inputs to and the outputs from the cerebellar cortex. In addition, their axonal synapses with the granule cells provides a neuroanatomical basis for reverberating activity in the cerebellar cortex (granule cell - Golgi cell - granule cell, a "short loop;" and granule cell - Purkinje cell - Golgi cell - granule cell, a "long loop").

Each granule cell, mentioned above, has three to six dendrites which terminate in claw-like formations. They receive inputs from the Golgi cells, as already described; they also receive inputs from the mossy fibers, one of the two major inputs to the cerebellar cortex. It has been estimated (Fox, 1962) that there are between 3,000,000 and 7,000,000 granule cells per cubic millimeter of granule cell layer.

The overall flow of data through the cerebellar cortex can now be reviewed. Input signals enter the cortex via the mossy fibers (originating outside the cerebellum) and the climbing fibers (origin unknown). Mossy fiber signals are transmitted to the granule cells, while climbing fiber signals are transmitted to the Purkinje cell bodies, as well as to Golgi cells and basket cells.

The output signals from the granule cells are transmitted to two major terminals. The first, reached via the parallel fibers, consists of the spines of the Purkinje cell dendrites; an enormous divergence characterizes this distribution. The second, also reached via the parallel fibers, consists of Golgi cells. This distribution has a moderate amount of divergence. A neuroanatomical basis for a "short loop" of reverberating activity is provided here, since the Golgi cell axons are connected to neighboring granule cells.

Climbing fiber signals, besides being transmitted directly to Purkinje cell bodies and to Golgi cell dendrites in the molecular layer, are also transmitted to basket cells in that layer. The axons of these cells, branching into a rectangular "grid," terminate in "baskets" which embrace about 240 Purkinje cell bodies. Again, there is an enormous amount of divergence.

Each Purkinje cell, with the three major inputs from climbing fibers, granule cells, and basket cells, is the locus of an enormous amount of convergence. Their outputs, in addition to being transmitted to the cerebellar nuclei, are also transmitted via recurrent collaterals to Golgi cells, as well as to neighboring Purkinje cell bodies. There is thus provided a neuroanatomical basis for feedback regulation of neighboring Purkinje cell output, as well as for a "long loop" of reverberating activity via Golgi cell to granule cell to Purkinje cell.

From a neuroanatomical standpoint, perhaps the outstanding characteristic of the cerebellar cortex is the tremendous amount of divergence in its synaptic fields. This provides for a vast amount of parallel data processing, in contrast to the serial mode of data processing characteristic of most computers. This enables the cerebellar cortex to subject its input neurograms to a vast number of transformations simultaneously, selecting from its enormous manifold of response patterns those momentarily appropriate for fulfilling its functional roles.

These functional roles may be divided into three distinct, but interrelated, processes: vestibular maintenance of poise, under stationary and dynamic conditions; coordination of biomechanical control units in complex patterns and sequences of movement; and integration of postural mechanisms in support of voluntary movement.

Vestibular Maintenance of Poise

From a mechanical standpoint, the human body is superbly balanced. The arches of the feet, the pelvic girdle, the supple yet strong vertebral column, the articulation of the skull with the cervical spine, and various other features of skeletal organization, all embody sound principles of structural design. In addition, bone is a living tissue, capable of adapting to variations in the chronic pattern of stress imposed upon it. As a result, in stationary postural configurations such as standing or sitting, surprisingly little muscular activity is required.

However, the enormous range of locomotory maneuver available to the human organism inevitably means that the body frequently is placed in situations in which it is wholly or partially off balance, or in which a threat to poise exists. A variety of neuromuscular mechanisms exists which function to maintain or to restore body poise. These can be divided into three groups:

a. Anticipations. To a large degree, especially in goal-directed locomotions, the nervous system has the capability of predicting when poise will or might be disturbed. To this capability is added that of generating adjustments in muscular tone which anticipate such potential disturbances of poise or "poise threats." These adjustment may take the form of direct or internuncially mediated increases in tonic activity of the α motoneurons which innervate these muscles whose action would tend to minimize the disturbance to poise. Or they may take the form of changes of γ bias on the muscle spindles of certain muscles, increasing the responsivity to poise disturbances of the myotatic reflexes involved.

b. Adjustments. As goal-directed locomotions occur, concomitant changes in the distribution of muscle tone are produced. These changes have the effect of preventing disturbances of poise or of minimizing such disturbances. These shifts in "body attitudes" are produced by neural networks, largely located in the brain stem, but under cerebellar regulation and control.

c. Reactions. Erroneous predictions or unforeseen eventualties may occur in connection with goal-directed locomotions or otherwise, which have the effect of producing disturbances of body poise. A number of complex mechanisms exist, which are actuated when poise deviation exceeds a certain threshold, and which strongly pre-empt the "final common path" of α motoneurons to restore poise. There may be a "velocity threshold" as well as a "displacement threshold" from equilibrium for these postural reactions to occur.

The major source of sensory data for these mechanisms appears to be the semicircular canals and otolith organs of the inner ear, although proprioceptors, especially in the muscles of the neck, also play a role. The vestibular nuclei of the brain stem provide the basis for an integrating neural network through which these mechanisms operate, with the flocculonodular node of the cerebellum providing a control center.

Coordination of Voluntary Movements

The tremendous variety of combinations and sequences of biomechanical control unit motions available to the human brain require an intricate coordinating system if unit motions are to be converted into meaningful patterns of movement. The cortico-ponto-cerebellar path, and its feedback loop via the red nucleus and thalamus to motor cortex, provides the neural basis for such coordination. The cerebellar cortex, especially that of the posterior lobe, constitutes the data processing network for this system. Sensory data from proprioceptors, cutaneous receptors, the visual system, and the auditory system are utilized by this data processing network. The commands issued by this system take the form of patterns of facilitation and inhibition superimposed on primary motor commands, coordinating the timing, the order, the direction, and the delivered force of the ensuing unit movements. Here is a multivariable system of great complexity, whose mode of operation is as yet very little understood. About all we can say is that the elegance and precision of organization of the cerebellar cortex is matched by the complexity of the functions it is called upon to perform.

Postural Integration in Support of Movement

Voluntary movement is like the main theme played by a symphony orchestra; it is based on a background of postural support which is not unlike the harmonic background and percussive rhythm of the orchestra. If a ball is thrown or a blow is struck, the whole body is involved in support of the act. An injury to the big toe of Dizzy Dean compelled a slight change in his pitching motion which resulted in a "sore arm" and the end of his baseball career.

The integration of postural mechanisms in support of movement is related to the maintenance of poise, but is nonetheless a distinct control mechanism. Postural support may actually disturb poise if the movement supported requires, as demonstrated by an end diving to catch a football.

Other components of the central nervous system may also be involved,* but the cerebellum evidently plays a major role. The cerebellar cortex of the anterior lobe appears to be the major data processing center of this system. Proprioceptive inputs from all over the body, as well as auditory and visual inputs, are operated upon by this center. The output goes chiefly to the reticular system of the brain stem, whence it is relayed to the appropriate motor control channels.

Both from a functional standpoint and from a neuroanatomical standpoint the cerebellar cortex is thus seen to be a data processing system of impressive character. What electrophysiological evidence do we have of its mechanism of operation?

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*Notably the extrapyramidal system.

Several gross electrical patterns have been observed. The first is a periodic oscillation of a frequency of about 150 to 200 cycles per second (Adrian, 1935; Dow, 1938). This rhythm has been localized to the Purkinje cell layer of the cortex (Brookhart et al, 1951).

A second pattern observed has been a much slower periodic oscillation of 8 to 12 cycles per second (Cooke and Snider, 1954). This appears to be related to activity in the cerebral cortex. The frequency corresponds to that of the α rhythm of the electroencephalogram.

Arduini, Borazzo, and Brusa (1955) have also described sustained negative shifts of the steady level of potential at the cerebellar surface. These occur as a result of peripheral nerve stimulation. They last for one to three seconds after single shocks to peripheral nerve.

The response of single units (believed to be Purkinje cells) has been studied by Brookhart et al (1950). A relatively high rate of spontaneous activity was observed, the units firing continuously or in repetitive bursts, at frequencies of around 70 to 80 cycles per second. This activity could be increased or decreased by stimulation of peripheral receptors or the cerebral cortex. A tendency to long "after-discharges" was noted following a period of excitation. Henneman (1961) has likened this behavior to modulation of "carrier" frequencies of FM radio signals.

It is evident that we still know very little about the detailed mechanism of action of the cerebellar cortex.

EXTRAPYRAMIDAL STABILIZATION OF BIOMECHANICAL SERVOMECHANISMS

As every control system engineer knows, stabilization of servomechanisms is a major problem in their design. There is no a priori reason for a particular combination of electrical and mechanical components to exhibit stability in its performance as a system. Fortunately, powerful analytical techniques are available which enable the engineer to ensure that system performance will be stable under all foreseeable operating conditions.

In the case of biomechanical servomechanisms, the situation is far more complicated. With perhaps a few special exceptions, almost all biomechanical control units appear to be intrinsically stable. But these units do not operate independendently of one another. Even under relatively quiescent conditions, they are interrelated in a complicated web of interactions. Moreover, for the enormous variety of locomotory maneuvers available to the brain, these units may be combined in temporary hookups (like breadboards) of considerable variety. Under such circumstances, the probability of unstable combinations is appreciable.

The central nervous system solves this problem by what might be called the Principle of Compensatory Stabilization. This is imbedded in a special group of neural components which, for historical reasons having little contemporary relevance, are usually referred to as the Extrapyramidal System.

Compensatory stabilization of combinations of biomechanical control units is not the only function of this system, but it is a major one.*

The types of instability exhibited under certain conditions by biomechanical control systems include uncontrollable oscillations (tremors) of a type familiar to control engineers. But they also include other varieties which are quite bizarre in their manifestations. Even classical forms of nonlinear instability do not appear adequate to account for some of these manifestations.

The term "extrapyramidal system" is a neuroanatomical term denoting all motor channels exclusive of the pyramidal tract in the medulla. From a functional standpoint, this definition is not very helpful. There are, however, a group of structures which, according to various observers (Martin, 1959), constitute a functional group. These are:

1. The corpus striatum, consisting of the caudate nucleus and putamen
2. The globus pallidus
3. The subthamalic nucleus
4. The substantia nigra

The corpus striatum and globus pallidus are relatively large nuclear masses deep in the white matter of the cerebral hemispheres. The substantia nigra and subthalamic nucleus are located in the brain stem. The major channels of communication among these structures are diagrammed in Fig. 28.

According to Jung and Hassler (1960), the main input to the corpus striatum comes from the centrum medianum of the thalamus. This nucleus in turn receives inputs from the reticular system of the brain stem and from the emboliform nucleus of the cerebellum. Various other thalamic nuclei also are connected to the corpus striatum (Crosby et al. p. 368).

The corpus striatum is relatively independent of the cerebral cortex; nevertheless, a number of inputs from the cortex have been described. These are relatively small, and probably originate chiefly in the premotor cortex of the frontal lobe (area 6).

Segundo and Machne (1956) have reported microelectrode studies of single units of the putamen. They found that such responded to various somatosensory stimuli from skin and muscles, as well to vestibular stimuli. Both activation and inhibition was observed; other sensory modalities were poorly represented.

Another major input (or feedback) comes from the substantia nigra. This transmits signals to the putamen and also to the globus pallidus (Crosby et al. p. 372). A feedback channel from the subthalamic nucleus has also been described. (Crosby et al, p. 376).

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*Another major function, discussed above is postural integration in support of movement, in conjunction with the cerebellum.

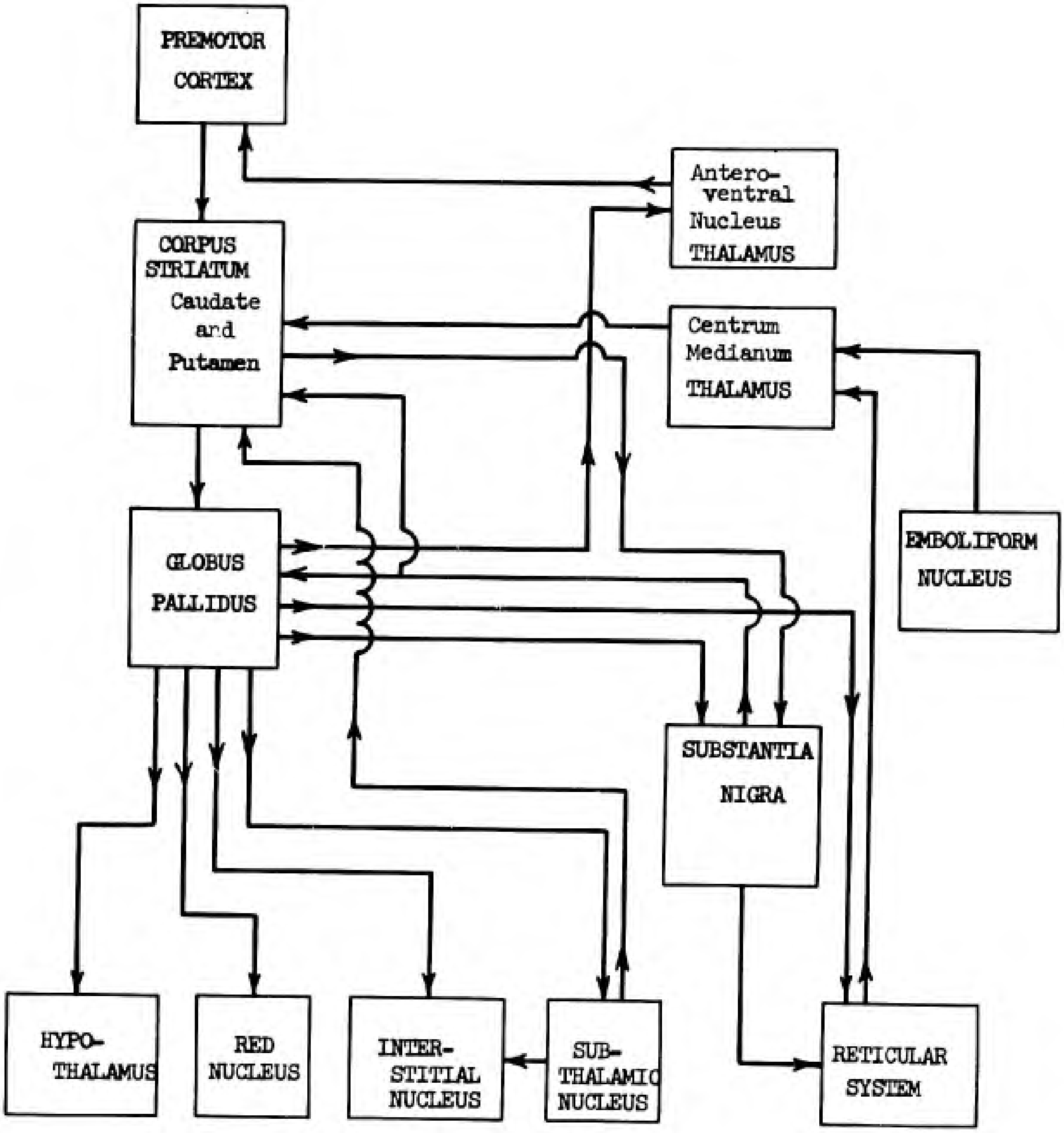

Fig. 28. Extrapyramidal system.

The outputs from the corpus striatum and globus pallidus are rather complex. Both the caudate nucleus and putamen project massively to the globus pallidus. Most of the outputs from this system come from the globus pallidus, but some also come directly from the caudate nucleus and putamen. These outputs, which go to a number of major nuclei, include:

1. The substantia nigra
2. The subthalamic nucleus
3. The reticular system
4. The hypothalamus
5. The red nucleus
6. Interstitial nucleus

In addition, there is a major loop which transmits signals via the thalamus to the premotor cortex.

The substantia nigra is a relatively large nucleus extending through a large part of the brain stem. It gets its name from the presence within its cells of the pigment, melanin. There is reason to believe that a significant fraction of its connections are still unknown. It receives inputs from the basal ganglia (corpus striatum and globus pallidus) and cerebral cortex. Its major known outputs are to the reticular system and back to the corpus striatum. Functionally, it appears to be a major control center of the γ motoneurons.

The subthalamic nucleus is a lens-shaped structure located below the thalamus. It receives inputs from the globus pallidus and projects outputs to the interstitial nucleus and other parts of the brain stem. Lesions of the subthalamic nucleus are associated with a neurological condition called hemiballismus, described below.

Very little is known about the detailed mechanism of operation of the extrapyramidal system. Much of our knowledge is derived from clinical disorders associated with lesions of various parts of this system. The phenomena observed in such disorders are the manifestations of motor functions as they occur in the absence of parts of this system. In most cases these phenomena have characteristics which would lead a control system engineer to infer instability of biomechanical control systems left intact. Some of the phenomena observed are the following:

1. Postural tremor (tremor-at-rest, static tremor). This is a fine, regular tremor, usually most marked in the distal limb, with a frequency of about four to eight cycles per second. Electromyographic studies show it to be characterized by alternating contractions in anatagonistic muscles -- for example, the biceps and triceps in the upper arm. The tremor disappears when the patient is asleep. It also disappears during voluntary movement

of the limb. It is exacerbated by strong emotion. Interestingly, severing the dorsal roots of the spinal cord, which interrupts the feedback reflex path from muscle spindles and other receptors, does not abolish the tremor. The mechanism of the tremor is unknown, but it appears in diseases in which the basal ganglia and substantia nigra are damaged.

2. Athetoid movements. These are involuntary movements which chiefly affect the peripheral muscle segments of the limbs and the face. They are usually described by such adjectives as "slow," "worm-like," "sinuous," "writhing," etc. They are less regular than a tremor; each muscle of the group affected appears to contract at a rate independent of the others, with spasmodic contractions common. Lesions of the corpus striatum and globus pallidus are frequently found.

3. Choreiform movements. These are involuntary movements involving muscle groups of the extremities, trunk, or head. They are described as rapid jerks or fragments of movement which appear purposeful and well coordinated, but which are unpredictable by the patient. Their coordinated character often enables the patient to disguise their involuntary character by completing the movement voluntarily or integrating it with some other action. They are enhanced by emotional stress, sensory stimuli, and voluntary activity. The maintenance of posture is rendered difficult by their occurrence. Lesions in the corpus striatum are associated with this condition.

4. Ballistic movements (ballismus, hemiballismus). These are violent, flinging (ballistic) movements involving most strongly the proximal muscles of the arms and legs. Frequently they involve only one-half of the body (hemiballismus). They come on suddenly and with such force that the patient may fall. An attack usually lasts for a long time. Lesions in the subthalamic nucleus are involved.

5. Festination. This is a characteristic gait observed in Parkinsonism. The patient moves forward off-balance, as if he were chasing his own center of gravity. His steps are short and his gait shuffling. One gains the impression that the neural networks controlling gait are operating in an unstable state.

There are a number of other characteristics of diseases involving the extrapyramidal system; the foregoing have been selected as exemplifying the major types of instability associated with these disorders. These phenomena, and others based on experimental studies, indicate that a major function of the extrapyramidal system is to stabilize biomechanical control systems in the enormous variety of "hookups" and "load conditions" to which they are subjected.

PROLEGOMENON TO A THEORY OF TELEOGENETIC SYSTEMS

Gibson (1963) has defined a "hierarchy of automatic control" which includes from lowest to highest level of sophistication the following "ranks":

1. Open-loop control
2. Conventional closed-loop control
3. Adaptive control -- including systems capable of modifying their own parameters to yield optimum performance with respect to one or more indices of performance under a variety of conditions not all foreseen
4. Automata which learn -- including systems which have the capability of recognizing familiar features about a situation and using stored information to deal with it

It appears to the present author that a category of automatic control still higher than any thus far seriously considered by control engineers is possible. It is proposed that systems in this category be referred to as teleogenetic systems. Such systems would embody a feature of the central nervous system not yet incorporated in engineering control systems: the capacity to generate its own goals.

The behavior of each existing category of automata can be described as "goal-seeking" (Rosenblueth, Wiener, and Bigelow, 1943). The input to the system can be characterized as a goal signal, and the system itself as a teleological mechanism which operates in such a way that the system output conforms to the goal, with minimum error. Even automata which learn can be characterized in this manner; in all cases the goal signal is given (it either is "designed into" the system as a set point, or it is provided for the system from some external source -- in the last analysis, a human being).

In the following a brief outline of a teleogenetic system is sketched. No attempt will be made to develop a rigorous mathematical theory of such a system, or to specify in terms of hardware its realization. It is believed that both are within the reach of existing mathematical knowledge and engineering technology.

A block diagram of such a system is given in Fig. 29. A teleogenetic system, as here conceived, consists of the following components:

1. A set of primary servos. These are ordinary closed-loop servomechanisms, each of which receives a goal signal and controls an output quantity. The output quantities are subject to unknown load conditions. Adaptive servomechanisms may be used without essentially altering the overall function of the system.

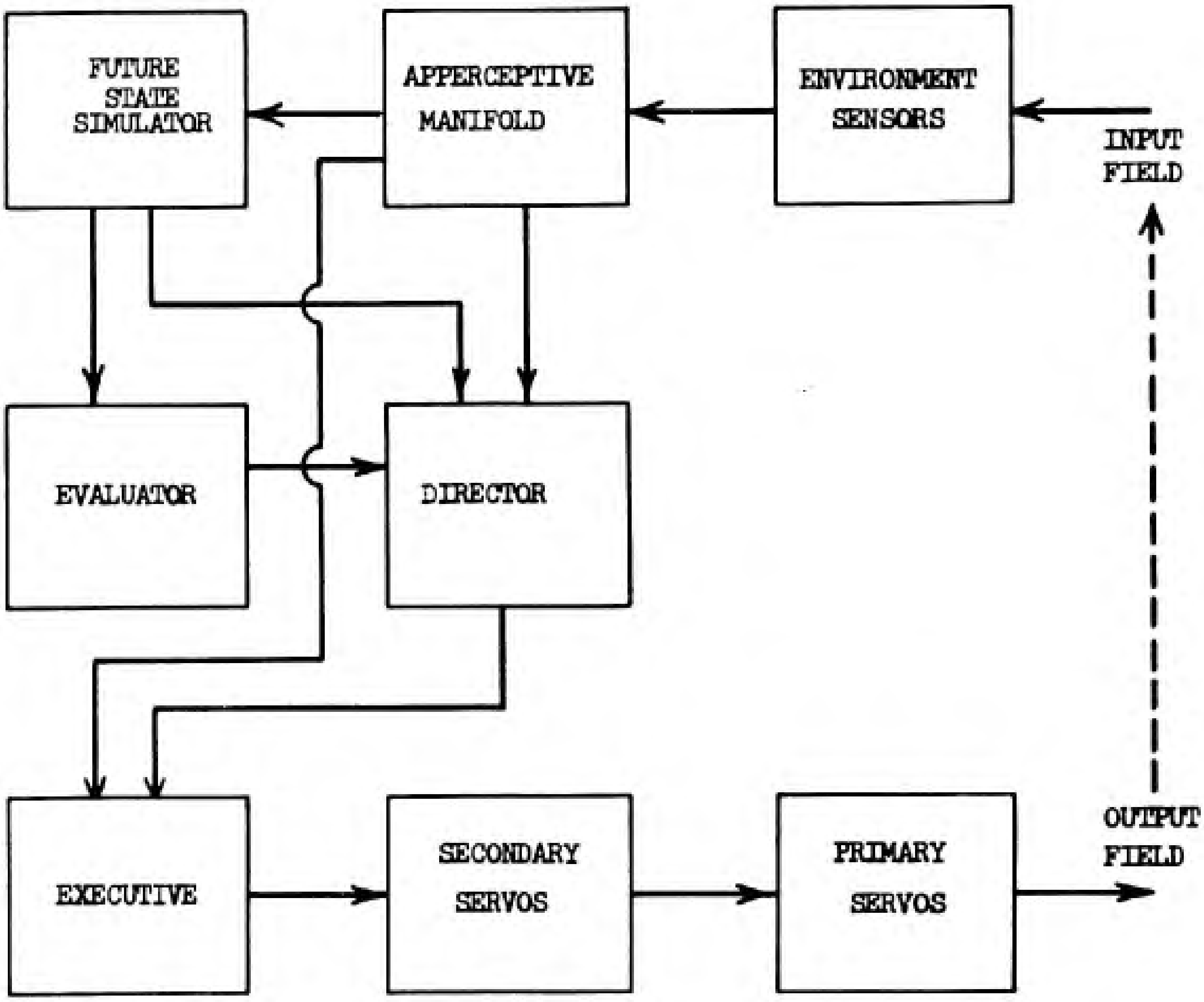

Fig. 29. A teleogenetic system.

2. A set of secondary servos. These are not organized into a fixed structure, but include necessary components and a "patchboard" which provides the capability for (automatic) connection of components into a variety of possible networks. They provide sequences and combinations of goal signals for the primary servos, and are "switched" into appropriate networks by "topological commands" from another major component, the executive, described below. Once "hooked up," they generate a program of goal signals in accordance with "generic goal commands" supplied by the executive.

3. An executive. Essentially a computer, the executive determines the topological structure of the secondary servos essential for adequate fulfillment of the "master goal" it receives from the director, another major component, described below. The executive also determines generic goals for the secondary servos, in accordance with the master goal and data received from another major component, the apperceptive manifold, also described below.

4. A director. This is the decision-making component of the system. The system as a whole may function in either of two modes of operation: Search Mode and Action Mode. One function of the director is to determine mode of operation.

In Search Mode, the system is not "committed" to a master goal. The executive and the primary and secondary servos under its control are "idling" in this mode. Other components of the system perform functions as described below.

In Action Mode, the system is committed to a master goal. The executive and its subsidiary servos function as described above, until the master goal is fulfilled. When this occurs, as determined by the executive, the executive so informs the director and automatically suspends action -- shifting to Search Mode.

A second function of the director is to determine master goals. This is done during Search Mode, and can best be described after the other major components have been discussed.

5. A set of environment sensors (or input elements). These detect (or receive) input quantities which may be, for convenience, represented as functions of time, $X_i(t)$.

6. An apperceptive manifold. Essentially a computer, this component receives the sensed inputs $X_i(t)$, and operates upon them to generate a set of quantities P_j called "perceptions." These might be functionals of the X_i's, or invariants of a set of transformations of the X_i's, or binary quantities which, for example assume the value 1 when $X_1 + X_2$ exceeds a threshold 5, and 0 otherwise. The important point is that the perceptions P_j are derived quantities, and that the system functions in terms of these quantities -- expressing its "goals" in terms of them, rather than the primary inputs.

7. A future-state simulator. This component is also a computer. It receives the P_j's from the apperceptive manifold, and has the capability of predicting their future at any time. However, the performance of this is more subtle than may at first appear.

The future-state simulator also has access to the "moves" available to the teleogenetic system. These moves are the ranges over which the output quantities Y_k may roam, and the set of primary goals, generic goals, and master goals available as described above. The future-state simulator not only can predict the future "state" of the P_j's while the system is in Search Mode, on the basis of the stochastic properties of the X_i's, it can also predict future states of the P_j's when the system "moves" in any of a set of possible Action Modes. This capability might require a computer of significant capacity, and it may be necessary to restrict the moves used for computing futures. In any event, prediction of futures under various simulated moves of the system is the major function of the future-state simulator, an operation in which the X_i's become not only functions of time but also of the outputs Y_k.

8. An evaluator. Also a computer, this component assigns "worth values" to each P_j, or to finite sequences of P_j's. The worth values may be +1 for positive worth, 0 for indifferent worth, or -1 for negative worth. The evaluator also computes "worth functions," summing worth values over specified time intervals for P_j sequences generated by the future-state simulator for particular moves.

An added sophistication which is probably desirable for the evaluator is to endow it with a learning capability, so that on the basis of its "experience" it could store in the memory certain worth functions associated with recurrent P_j sequences. This would probably be economical in its running time.

The director is designed (or programmed) to make decisions whenever worth functions associated with certain moves exceed a given threshold. It may also select, from optional moves, that move which has the highest worth function. When it makes a decision, it switches the system to Action Mode, and generates the master goal signal appropriate for the move selected.

This sketch of a teleogenetic system is admittedly incomplete, and other schemes for systems of this category are certainly possible. It does illustrate a way in which an existing capability of the central nervous system -- the ability to generate its own goals -- can be realized technologically. In view of the growing complexity of military weapons systems, aerospace systems, and computer-controlled industrial systems, the development of teleogenetic systems may soon become necessary. If so, the biological prototype of such a system is available for further study.

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13. ABSTRACT

A study was made of the central nervous system from an information processing point of view. The study entailed a review and critical analysis of several hundred references, and involved a considerable amount of recasting and reorganization of existing knowledge into the terms and concepts of engineering, with particular reference to potential bionic applications. The study was selective rather than comprehensive. The neural coding problem was first examined, the history of efforts dealing with this problem was reviewed, and a mathematical representation of neural signals (neurograms) and neural operators was formulated. The processing of data by the visual system was then described, with particular reference to form, color, and movement detection, the temporal continuity of visual objects, image fixation, automatic focussing control, intensity control, image fusion, depth perception, and the stabilization of visual space. Next, the neural control of movement was analyzed from a servomechanical viewpoint. The unit biomechanical control system was defined, and the corticospinal command of this unit system was discussed. The cerebellar coordination and extrapyramidal stabilization of sequences and combinations of biomechanical control unit actions was examined. Finally, the ability of the central nervous system to generate its own goals——a capability for which no technological counterpart yet exists——was discussed, and a preliminary sketch of a theory of teleogenetic systems was presented.

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14. KEY WORDS	LINK A		LINK B		LINK C	
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