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Translation

ARTIFICIAL SENSE ORGANS

PROBLEMS OF MODELING SENSORY SYSTEMS

By

S.V. Fomin, Ye. N. Sokolov and G.G. Vaytkyavichyus

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Moscow ISKUSSTVENNYYE ORGANY CHUVSTV. PROBLEMY MODELIROVANIYA SENSORNYKH SISTEM in Russian 1979 (signed to press 15 Jun 79)

[Book by Sergey Vasil'yevich Fomin, Yevgeniy Nikolayevich Sokolov and Genrikh Genrikhovich Vaytkyavichyus, Izdatel'stvo "Nauka", UDC 519.95]

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ANNOTATION

This book deals with construction of artificial human and animal sense organs. The analyzer systems, in which there is a mechanism for enhancing differential sensitivity, codes the stimulus with the number of the most stimulated channel. Analyzers of intensity, color, orientation, line of direction and speed of movement of an object, its position in space are described.

This book is intended for neurophysiologists, biophysicists and specialists in sensitizing robots.

There are 74 figures; bibliography lists 111 items.

FOREWORD

This book is the result of 15 years of work using methods of psychophysics, neurophysiology and cybernetics. The research was conducted in a man-neuron-model system. Investigation of a concrete sensory function on the psychophysical level, in experiments on man, developed in the direction of demonstrating its neuronal mechanisms in animal experiments. The final stage of the study was a model, for which rather rigid requirements were imposed; the entire model reproduced the psychophysical characteristics of the function under study, while each neuron-like element of the model reproduced the characteristics of the corresponding real neuron.

Construction of the models was based on the neurophysiologically validated principle of coding a signal by the number of the detector channel. This principle provided for combining data transmission and processing in a large number of parallel channels.

The study of concrete analyzers of color, intensity, motion, orientation and depth made it possible to formulate general principles of construction of artificial sense organs out of neuron-like elements. Expressly these general principles of construction of artificial sense organs, with the features of natural neuronal analyzers, constitute the main content of this book.

Adhering to the principle of coding by channel number in artificial sensory systems, it is necessary to settle the question of using information presented in this manner in problems of control. Electrophysiological studies of command neurons, which generate "chords" of motions by means of their systems of communication with motoneurons, made it possible to conclude that control problems are solved by connecting or disconnecting detectors from command neurons. The results of this analysis were formulated in the description of the conceptual reflex arc.

The aggregate of receptors, primary detectors and selective secondary detectors forms the neuronal analyzer. This analyzer is an expression of the biological analyzer discovered by I. P. Pavlov. An exogenous signal, which elicits a set of excitations in independent primary detectors, generates an excitation vector. The excitation vector, which acts upon the "fan" of communication [or connection] vectors that connect primary and secondary detectors, creates single maximum excitation on one of the elements of the population of secondary detectors, coding the signal with the localization site of the excitation maximum.

According to the principle of coding a signal by channel number, a set of stimuli is reflected in an n-dimensional sphere, which is formed by the detector neurons. With a change in signal, the excitation maximum reflecting the signal change shifts over the quasireceptive surface represented by a set [or many] secondary detectors.

Reflection of the signal on the sphere leads to a new approach in human psychophysics and metrics of robot perceptive space. The subjective difference between stimuli in man and a robot equipped with neuronal analyzers is measured by the small arc of the large circle of the *n*-dimensional sphere. This arc connects points at which are localized the secondary detectors representing the corresponding stimuli.

The precision of function of the human and animal neuronal analyzer is enhanced as a result of operation of adaptation mechanisms of primary detectors and lateral inhibition of homologous primary detectors referable to different local analyzers. The emphasis of differences between signals is manifested by successive and concurrent contrasts. Introduction of adaptation and lateral inhibition into artificial sense organs providing for enhancement of discriminant sensitivity generates illusions in them that are analogous to man's perceptive illusions.

Thus, artificial sense organs consisting of neuron-like elements reproduce very completely the structure and function of human sense organs. The general principles of construction of artificial sense organs from neuron-like elements may find practical applications in two different fields: development of sensory prostheses directly coordinated with the neuronal structures of the human brain and design of sense organs for robots with elements of artificial intelligence.

Regrettably, Sergey Vasil'yevich Fomin, whose ideas served as the basis of this book, passed away at the final stage of preparing the manuscript and could not see it published.

CHAPTER 1. CONSTRUCTION OF ARTIFICIAL SENSE ORGANS

Robot's artificial sense organs. Development of modern technology is largely related to advances in creating integral robots with elements of artificial intelligence. The ability to function in a complex environment is a distinctive feature of such robots. For this, not only must they have a sophisticated system of actuating elements, but a well-developed system of artificial sense organs capable of processing a large volume of sensory data for analysis of scenes and complex acoustical signals.

There must be provisions for man's communication with robots for effective control thereof. We refer not only to development of an effective language for communication, but obtaining a similarity of internal conceptions of man and robot. In other words, it is necessary for objects distinguished in the environment by robot and man to coincide as fully as possible. Only then will the interaction of man and robot be effective. Finally, all deviations of internal conceptions of the robot from the internal conceptions of man should have a simple and graphic interpretation in terms of human perception.

All these considerations compel us to search for the means of creating artificial sense organs, the operating principles of which would be similar to the operating principles of human and animal analyzers. Since human and animal analyzers are capable of rapidly processing large arrays of input data, we can expect to find new effective means of information processing on this route.

Computer's perception organs. The area of refinement of systems of man's communication with a computer is an important area of application of artificial sense organs. Although all of the procedures of recognizing speech sounds and analyzing visual scenes can be implemented by computers, this would require a large memory and significant time for conversion of such complex signals. A better way would be to develop specialized parallel-action processors that would permit rapid processing of complex acoustical signals and visual scenes. Thus, the problem of creating artificial sense organs for a robot ties in with the problem of creating perception organs for a computer. It is also desirable to have the internal representations of acoustical and visual signals in the computer agree with the internal conceptions of man, so that the language of communication between man and computer would be based on the similarity of conceptions.

Prostheses of human sesne organs. In order to perform the task of creating acoustic and visual prosthesis directly related to neuronal mechanisms of the brain, it is necessary for the principles of signal coding in the prosthesis to conform with the principles of signal coding in the brain. Work on artificial sense organs based on biological principles enables us to come close to such agreement, since the reactions at the output of technological neuron-like elements are analogues of reactions of real neurons. Thus, development of artificial sense organs based on the functional principles of human and animal sense organs would also serve as the basis for developing new types of prosthetics of human sensory systems.

Man--neuron--model. Development of general theory of artificial sense organs providing for similarity of internal conceptions of man and robot is based on psychophysiology, which emerged on the borderline of psychology, physiology of higher nervous activity, neurophysiology and cybernetics. Psychophysiology is the discipline that deals with neuronal mechanisms of psychological processes; it is based on the man--neuron--model principle. As they analyze functions on the level of human behavior and verbal reactions, psychophysiologists turn to analysis of neuronal mechanisms implementing this function. The work ends with construction of a model of the function under study. The model is created with neuron-like elements. Rigid requirements are imposed on the model: the model as a whole must recreate the function under study on the behavioral level, while its neuron-like elements must conform in characteristics to real neurons involved in the modeled function. From the standpoint of development of artificial sensory systems where internal conceptions of man and robot would coincide, such a model of a sensory function is also a technical solution of the problem.

A comparison of concrete models of sensory systems makes it possible to construct a single scheme--generalized model of sensory functions. It is possible to construct artificial sensory systems that have no direct biological prototypes on the basis of such a generalized model.

Information coding in the nervous system. The nervous system performs functions of control, transmission and processing of incoming information. Incidentally, it should be borne in mind that the above separation is quite arbitrary, since control always includes some information processes, whereas the organs that transmit and process information serve as objects of control (for example, perception of visual information depends appreciably on control of eye movements). Moreover, there are many general principles, such as multilevel organization and learning ability, are inherent in processes of control and information processing.

The same flow of signals transmitted over a communication line can deliver different information, depending on expressly what the corresponding receiver reacts to. For example, when we receive a letter we are usually interested only in its text. However, it is conceivable that two individuals who are corresponding agreed to attribute meaning to, for example, the color of the paper or lettering, rather than the text of the letter. One can select such "informative signs" arbitrarily; but the receiver must have the physical properties to perceive them (the color of the paper would mean nothing to a blind person) and to retain them in the course of transmitting the message (how the letters are written cannot serve as the code if we use telegraphy, rather than the mails).

These obvious considerations are quite applicable to transmission of information in the nervous system also. Our perception of the world around us is multifaceted. We perceive bright colors, diverse sounds, odors and peculiar shapes in it. In the nervous system, all relevant information is coded by a specific distribution of excitations in numerous neurons. The question of expressly how this coding is done is one of the basic ones in neurophysiology and biophysics of complex systems. Let us consider two problems, namely, coding information by a series of impulses within a single (unbranched) nerve fiber and coding in a complex multichannel system.

Coding information in a nerve fiber. It is a known fact that the interspike intervals serve as information carriers when a series of impules extends over a nerve fiber, since spikes themselves are rather standard. But what precisely is significant: the length of different intervals, their mean length over a certain segment, grouping of impulses in a bundle or something else? This is far from clear, and one could hardly offer a single answer that would be suitable for all cases.

At first glance, it appears best to code information by the lengths of different interimpulse intervals, similar to the dots and dashes of the Morse code. This method could provide for a high throughput of the communication channel and high speed of system operation. Coding information with the average frequency of impulsation or some other statistical characteristics of a series of impulses cannot provide such rapid action. However, there are several factors that limit the possibility of coding information by the lengths of different interspike intervals. These factors include, among others, the following.

Mathematical modeling of processes of dissemination of excitation in a nerve fiber [1] and direct physiological experiments have shown that the impulse sequence, which has a complex structure, does not retain this structure as it travels over a long nerve fiber if the impulse frequency in a train is high enough. This effect is attributable to the dependence of velocity of impulse propagation over the nerve fiber on duration of the refractory phase, i.e., time that has elapsed after the preceding impulse. By virtue of this dependence, there is gradual equalization of interspike intervals in a train of spikes, and only information about the mean impulse frequency is retained at the output. Of course, this does not happen when impulses follow one another at long enough intervals, since none falls into the phase of relative refractoriness of the fiber. But then the information is transmitted slowly, and the main advantage of coding by individual intervals, high throughput, is lost.

These considerations apply mainly to long fibers. Similarly to exponential extinction of potential in a cable, there is exponential leveling down of information about the duration of individual interspike intervals in a long fiber. In short fibers, the shape of the impulse train does not have time to level down, even when frequency is high.

It should be borne in mind that dissemination of impulses over a fiber in a relatively refractory state cannot be construed as a purely laboratory phenomenon observed with unnaturally high stimulation frequencies. The phase of relative refractoriness lasts about 100 ms and the interpulse interval constitutes only 6-10 ms in the motor axons of the locust. In the internuncial neurons of the spinal cord of mammals, in the neurons of certain ascending tracts and acoustic nerve fibers frequencies of up to 100 imp s^{-1}, and in fibers innervating the electrical organs of fish the frequencies are even higher, up to 1500 imp s^{-1}. Thus, the propagation of impulses over a fiber in a relatively refractory state is certainly encountered under natural conditions.

Smoothing of interpulse intervals is one of the reasons that limit coding by the lengths of different intervals. Another reason is referable to the distinctions of the decoding system. Secretion of mediator in synapses in response to an impulse is stochastic in a number of instances. There is a probability of only 1/2 that an impulse going to motoneurons over group I fibers will elicit secretion of mediator. It is obvious that in such a case it becomes unrealistic to consider the possibility of coding information by individual interimpulse intervals.

These circumstances limit the possibilities of coding information in a nerve fiber with individual impulses. However, such coding is by no means ruled out, particularly in short fibers. Thus, as far back as the early 1960's, in several well-known studies conducted with neurons of the Aplysia mollusk, it was demonstrated that one can obtain different responses from artificial stimulation of these neurons with pulse trains of the same average frequency but different configuration. For example, the neuronal reaction may change if this pulse train is delivered in reverse order. Evidently, in this and other similar cases, the neuron reacts to the temporal pattern of the pulse train as a certain whole [2, 3].

Coding information by channel number. Recent experimental and theoretical studies indicate that there is widespread so-called coding of information by the channel number, or locus [site] coding in a living organism, particularly its sensory systems. According to this conception, the sensory system has a set of detector neurons, one of which is stimulated more than its neighbors by a specific stimulus. The number of the detector neuron that is maximally excited determines the sensation that is elicited by the coded signal parameter (brightness, color, direction of movement). If two stimuli elicit maximal excitation of the same detector, they are not distinguished according to a given parameter.

It was demonstrated experimentally that the reaction of individual sensory neurons presents distinct specificity for the value of the parameter of the stimulus delivered [4-6]. In particular, some of the neurons of the visual analyzer do not react at all to diffuse illumination of the retina [7]. One must deliver an appropriately organized image to a specific part of the retina to elicit a reaction in such a neuron. The mechanism of lateral inhibition [8] provides for the high sensitivity of detector systems. However, in the opinion of the critics of the detector conception, detectors are temporary combinations of neurons that reflect only the process of "running" a certain program for pattern recognition through the neuronal network. After running this program, the "detector functions" of the cell may disappear and it could take on other functions.

Current experiments on stability of detector properties of neurons revealed that in individual neurons these properties are either genetically determined or formed in early ontogenesis, and then persist for the entire lifetime of an animal.

Coding by channel number as a process of parallel information processing by no means rules out successive analysis. If a stimulus is complex enough and the animal does not have to deal with it often, perception may proceed step by step, by isolating the important and simple features of the analyzed image. This is associated with successive activation of different detector neurons, which reflects the process of successive assembly of the "internal image" of an exogenous stimulus from simple tags [9, 10]. Such is the function, for example, of eye movements in perception of a complex image [11]. It should also be stressed that coding by channel number provides for concurrent transmission and processing of information. Concurrent ["parallel"] information processing enables living organisms to effectively solve identification problems.

A property of living systems, which we could call "functional stability," is also related to coding by channel number. We use functional stability to refer to viability, the capacity of a living system to perform its main functions, even if in a somewhat reduced form (for example, a dog could move satisfactorily on three legs, whereas a car missing a wheel cannot), in the presence of some injury, even rather significant. The concept of functional stability is related, to some extent, to the concept of reliability in the meaning of von Neumann, but does not coincide with it. In his well-known work, von Neumann [12] discussed the reliability of a system which, like an electric switch, has two states--on and off. A different situation is inherent in living systems, in that along with the two extreme states--complete work capacity and complete breakdown--there are also various intermediate states of partial work capacity. It is logical to introduce the concept of functional stability in the presence of injury for such systems. Evidently, the principles of constructing functionally stable systems must be other than Neumann's principles of reliability.

The combination of coding by channel number and appropriately organized lateral inhibitory connections could serve as the basis for constructing neuronal systems that are quite perfect in functional stability, although some elements of these structures do not have such perfection [13].

In conclusion, it should be indicated that information processing in neural networks is often described as follows: all processing occurs in neurons, while the nerve fibers that connect them play merely a passive, transmitting role. However, there is every reason to believe that this conception is not entirely correct. Let us consider the process of propagation of excitation over a branching fiber in the belief that this process is described by the well-known equations of Hodgkin-Huxley. As shown by estimates, the branching node of such a fiber could play the part of logic element, implementing certain basic logic functions of "or," "and" and "inhibition," depending on the conditions (proportion of diameters of fibers forming the ramification, difference in times of input signal in the unit via different fibers).

By combining the main logic functions one can obtain others. Here it is suggested that there are natural analogies with so-called homogeneous environments--technical equipment similar in properties to branching neural networks, which have recently gained rather wide popularity as the basis for construction of various computer systems.

Thus, even a single branching unit of a nerve fiber could perform rather complex physiological functions, for example, serve as a detector. The possibility of complex logical information processing in branching structures suggests that, perhaps, the role of dendrite arborizations in information processing is much greater than usually believed. With reference to neuronal nets, we are apparently oversimplifying the individual cell. Stating that "the brain is a computer," we relegate the modest role of a single element to a single cell. Perhaps the formula that "the neuron is a computer" is closer to the truth.

According to the foregoing, the function of detector could be performed by parts of a neuron, rather than the neuron as a whole. The material submitted below is not in contradiction with this conclusion, although the term "detector" implies a single element of the corresponding neuronal net. The combination of numerous independent detectors in a single element does not introduce any appreciable difficulty in considering the function of the entire analyzer.

CHAPTER 2. MODEL OF CHANNEL NUMBER CODING

Spherical model. The function of signal discrimination in a model of coding by channel number is provided by the fact that a specific value of parameter of an exogenous signal generates a solitary maximum of excitation on one of the specialized detector neurons. Detector refers to a neuron that is selectively adjusted for a specific value of the signal parameter. This selective adjustment of the detector is obtained by a specific system of communications, by which the detector is connected to neurons of the underlying level or receptors. Each detector forms one of the parallel channels for information processing. With a change in the exogenous signal, the maximum excitation shifts from one detector to another. If two signals elicit maximum excitation of the same detector, they are not distinguished. Schematically, a detector can be described as a formal neuron with several inputs through which signals come from underlying neurons--primary detectors or receptors. Each of the inputs should provide independent information to the detector (Figure 1). The independence of the inputs means that one cannot predict the activity of one input on the basis of knowledge about the activity of any other input.

The diagram illustrates a secondary detector. The arrow shows the direction of the signal at the detector output. The lines converging on the detector illustrate arrival of signals that converge on the detector (f_i--excitation coming over the ith channel). The small circles at the point of contact between the input and detector represent the coefficients of synaptic transmission; c_{ji}--coefficient of synaptic transmission of the ith channel on the jth detector. The dotted line refers to part of the inputs not shown on the diagram. The detector adds the paired products of each input signal multiplied by the corresponding coefficient of synaptic transmission:

$$d_j = c_{j1}f_1 + \dots + c_{ji}f_i + \dots + c_{jn}f_n = \sum_{i=1}^{n} c_{ji}f_i$$

where d_j is magnitude of excitation of the jth detector. The set of delivered stimuli forms excitation vector $F = \{f_1, \dots, f_i, \dots, f_n\}$. The set of communication coefficients forms the communication vector $C_j = \{c_{j1}, \dots, c_{ji}, \dots, c_{jn}\}$. The reaction at the detector output equals the scalar product of excitation vector multiplied by communication vector $d_j = (F, C_j)$. When the input signal changes, so does the neuronal reaction, and it reaches a maximum when the excitation vector is collinear with the communication vector. The modulus of the communication vector is constant $|C_j| = \text{const}$. If $|F| = 1$, $d_{j\max} = \cos [F, C_j]\ |C_j||F| = |C_j|$, ($j = 1, \dots, m$).

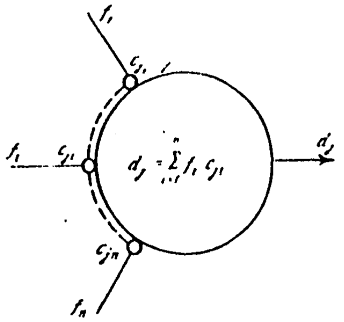

Figure 1.
Structure of a secondary detector

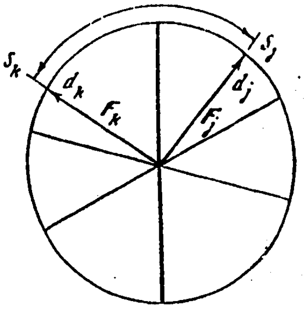

Figure 2.
Spherical model of signal discrimination

The detector is selectively adjusted for the signal whose excitation vector is collinear with the communication vector of this detector. In order to obtain a set of such detectors with maximum sensitivity to a change in parameter, excitation f_i as a function of the signal must be cosine curves. This means that either the receptors themselves must have such characteristics or that there must be elements to perform the necessary conversions between the receptors and secondary detectors.

Let us consider the case where a selective output detector receives signals from primary detectors. All of the primary detectors together, the number of which in the general case equals n, have independent sensitivity functions in relation to the coded signal parameter.

If a stimulus with preset value of coded parameter is delivered to the input of the sensory system, each of the primary detectors will be excited to a certain level. The magnitude of excitation of each primary detector can be viewed as vector coordinate. Let us call such a vector the vector of excitation. The number of independent coordinates of this vector determines its dimensionality. All information about the stimulus is contained in the set of excitations of primary detectors; in other words, it is determined by the excitation vector. In Euclidean space, the vector is characterized by direction and modulus (length). However, the vector modulus is not suitable for coding the values of stimulus parameter. Indeed, the vector modulus depends on intensity of the stimulus, whereas signal coding should not depend on stimulus intensity. Consequently, the value of the coded signal parameter must be coded by the direction of the excitation vector.

The direction of the excitation vector can be characterized by the point of its intersection of a solitary n-dimensional sphere. In the proposed method, the signal is coded by reflecting the physical (stimulus) space on the surface of the n-dimensional sphere (subjective space). The dimensionality of the subjective spherical space is smaller by one than the number of independent inputs and it equals $(n - 1)$.

Thus, a stimulus with specified value of parameter is represented by a point on a solitary n-dimensional sphere. When the stimulus changes, the point that represents it shifts over the sphere in accordance with the change in direction of the excitation vector. The more the stimulus changes, the farther the point shifts and the greater the subjective change in the stimulus. The shortest arc of the large circle between points on the n-dimensional sphere representing the corresponding excitation vectors is a gauge of the subjective distance between two stimuli (Figure 2).

The diagram illustrates the space in which is situated a sphere formed by a set of detectors; the kth detector is on the sphere $|C_j|$ = const at point d_k, which is obtained when this sphere intersects vector $F \| C_k$; the thin lines refer to the coordinate system. Two signals S_k and S_j generate two excitation vectors F_k and F_j. Maximum excitation of output detector d_k and d_j corresponds to each excitation vector. Thus, on the sphere each signal is represented by points d_k and d_j. The subjective difference between stimuli is determined by the arc of the large circle that separates detectors $\smile d_k, d_j$. This arc equals the angle between excitation vectors generated by each of the stimuli, i.e., $\smile d_k, d_j = \arccos (F_k, F_j)$.

If two stimuli induce two excitation vectors equal in direction they are not subjectively distinguished. Thus, a set of physical signals is projected on the surface of the sphere constituting the perceptive space of the stimuli. The dimensionality of the perceptive space is determined by the number of independent primary detectors. The threshold of discrimination between two stimuli equals the arc that separates two adjacent detectors. The magnitude of the threshold measured in angles is constant. However, the threshold measured in stimulus units may vary for different stimuli, depending on how the direction of the excitation vector changes with change in the stimulus. If we know the characteristics of primary detectors, we can calculate the subjective difference between stimuli. Conversely, if we know the subjective distances between stimuli and basis of space, we can find the characteristics of primary detectors.

Thus, in order to assess the subjective distance between two stimuli we must find the excitation vectors they generate and locate the points corresponding to the compared stimuli on an n-dimensional sphere, then draw a large circle of the sphere through these points and find the shortest distance on it. This gauge of subjective closeness of two stimuli is equivalent to the value of the angle between two excitation vectors generated by compared stimuli.

Characteristics of primary detectors. There is a point on the n-dimensional sphere of the model corresponding to each stimulus. If an orthogonal basis is specified, the position of the points on the sphere can be stipulated by its coordinates which, in the case of a solitary sphere, correspond to the cosine of the angle between corresponding basis vectors and the vectors determining the position on the sphere of the maximally excited detector. When the stimulus parameter changes, the coordinates of the points are described by the corresponding cosine curves.

The conclusion concerning the cosine curve characteristics of primary detectors can be obtained more strictly. The subjective difference between two stimuli is determined by the angle formed by excitation vectors: the wider the angle, the greater the subjective difference between stimuli. To provide high differential sensitivity for all stimuli one should select functions of primary detector sensitivity so that the angle between each pair of compared stimuli would be as wide as possible. To satisfy this condition and create an optimum differential sensitivity function for the entire system, the characteristics of primary detectors must be described by cosine curves, the argument of which is a certain function of the coded signal parameter (Appendix 1).

Thus, the characteristics of primary detectors must be cosine curves for the system of selective detectors to effectively distinguish exogenous signals.

Construction of secondary detectors. Schematically, we can describe an output detector as a formal neuron with several inputs. Each input is characterized by a certain efficiency of synaptic transmission which can be described as coefficient of communication. This coefficient determines the communication [relationship] between the primary detector or receptor and the secondary detector. A stimulus traveling over a given input to the detector is determined, on the one hand, by the force of delivered stimulation and, on the other hand, by the coefficient of synaptic communication. Thus, a signal passing from one of the inputs is determined by the product of force of arriving excitation multiplied by the coefficient of synaptic transmission. Analogous considerations are valid for other inputs. The detector sums up the stimulus arriving via all inputs. The overall reaction of the detector to the input signal equals the sum of products of excitation arriving over the input multiplied by the corresponding communication coefficient. The same can be expressed more concisely in the language of vector algebra. If all coefficients of communication [or relation] are viewed as components of the vector of communications and all stimuli arriving over inputs as components of the excitation vector, the detector's reaction equals the scalar product of excitation multiplied by the communication vector. If the communication vector of a given secondary detector is known by altering the signal and excitation vector induced by this signal one can determine the characteristics of the secondary detector. For this, the stimulation vector is scalarly multiplied by the communication vector fixed for this detector. When the excitation vector becomes collinear with the communication vector, the detector's reaction reaches a maximum. If we take this position of the excitation vector as the reference point, a decrease in reaction of output detector is observed when the excitation vector deviates from this position, measured in angles. Thus, the characteristics of the output detector are selective in relation to a specific signal (Figure 3).

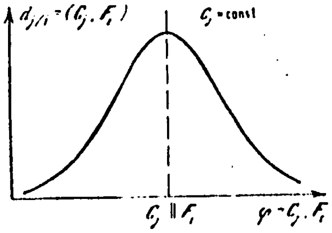

Figure 3.
Characteristics of secondary detector

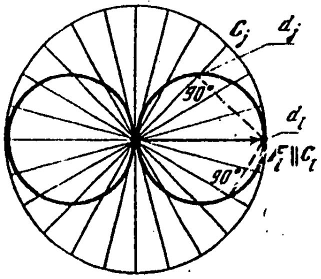

Figure 4.
Projection of excitation vector on fan of communication vectors of set of secondary detectors

Angle ϕ, which is formed by communication vector C_j of the detector and excitation vector, is plotted on the x-axis; the scalar product $d_{j/i} = (C_j, F(\phi_i))$ is plotted on the y-axis. Excitation vector $F(\phi_i)$ is a function of the input signal. Communication vector C_j is fixed for the given detector. The neuronal reaction reaches a maximum when the signal is at a level when the excitation vector is collinear with the communication vector of this detector. When the signal changes from this optimum level, the reaction of the jth output diminishes.

Since each output detector is related to all primary detectors, each secondary detector has its own communication vector. As a whole, the communication vectors of all secondary detectors form a fan of vectors in a space whose dimensionality is determined by the number of inputs. This can be graphically illustrated when each secondary detector has only two inputs (Figure 4).

A set of vectors of communications $\{C_j\}$, $(j = 1, \ldots, n)$ $|C_j|$-const corresponds to the set of secondary detectors. Each kth secondary detector has a corresponding communication vector C_k. An exogenous stimulus generates excitation vector F_l. Excitation that equals the scalar product of excitation vector F_l multiplied by the communication vector corresponding to a given detector arises on each of the secondary detectors under the influence of the stimulus. Thus, the magnitude of excitation of the jth detector induced by the $S_{\phi l}$ stimulus equals the value of the projection of vector $F(\phi_l)$ on the jth communication vector C_j. The figure eight shape shows the distribution of reactions of d_l detectors over their entire population: $D_l = CF_l$, where D_l is the column-vector $\{d_1, \ldots, d_i, \ldots, d_n\}$, $C = \| C_{ji} \|$ $j = 1, \ldots, n$; $i = 1, \ldots, m$.

The fan of communication vectors of a given set of detectors enables us to calculate the distribution of stimuli over the entire set of detectors with delivery of a fixed stimulus. Excitation of a secondary detector is determined by the scalar product of two vectors--excitation vector, which is constant in the case of a fixed stimulus, and communication vector, which each secondary detector has. By calculating the scalar product of a specified excitation vector multiplied by each communication vector, we can find the values of excitations of all detectors in the set. Together they form the excitation profile. Here, one of the detectors is maximally excited coding unequivocally the parameter of the stimulus (Figure 5).

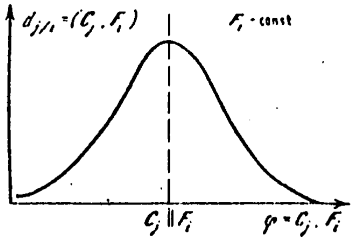

Figure 5.
Profile of excitation on a set of secondary detectors

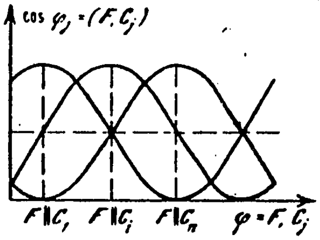

Figure 6.
Set of detectors as a multichannel correlator

Angle ϕ, formed by the excitation vector and communication vector of each secondary detector is plotted on the x-axis, so that the secondary detector number is also plotted on the x-axis. On the y-axis is the scalar product $d_{j/i} = (C_j, F_i)$ of each secondary detector communication vector multiplied by the excitation vector F_i = const going to these detectors. A maximum reaction occurs in the secondary detector for which the communication vector is collinear with the excitation vector. All other detectors respond with weaker reactions. Thus, the graph illustrates the profile of excitation on a set of secondary detectors under the influence of a fixed stimulus. The shape of the excitation profile for the entire set of detectors per fixed stimulus coincides with the characteristics of one secondary detector when the excitation vector changes.

The coincidence of characteristics of one detector with the profile of excitation of the entire set of detectors per fixed stimulus occurs with change in stimulus because the detector's reaction is determined by the scalar product of excitation vector multiplied by the communication vector. Calculation of the characteristic of one detector shows a change in excitation vector. With calculation of the excitation profile there is a change in communication vector. But the excitation vector is collinear with the communication vector of corresponding detectors, and they could replace one another in the scalar product.

According to the principle of signal coding by channel number, all communication vectors of a set of secondary detectors have the same moduli, so that in the case where there are two primary detectors at the input the ends of the communication vectors are on the circumference. Since the moduli of communication vectors are identical, each of the scalar products correct to within the constant factor [multiplier] equals the cosine of the angle between the specified excitation vector and corresponding communication vector. The detector whose communication vector forms a zero angle with the excitation vector will present maximum excitation. In other words, the communication vector of a secondary detector must be collinear with the vector of stimulation that this stimulus induces in primary detectors in order that the stimulus would elicit maximum excitation in the secondary detector. The number of the maximally excited detector determines unequivocally the direction of the excitation vector and, consequently, the stimulus that this excitation vector generates.

Set of detectors as a multichannel correlator. The reaction at the output of each secondary detector equals the scalar product of excitation vector multiplied by the communication vector or, correct to within the constant factor, the cosine of the angle between them. Thus, with change in the signal, the detector's response, which changes in the range of +1 to -1, calculates the coefficient of reciprocal correlation between the set of delivered stimuli and the set of synaptic connections. The entire set of detectors forms a multichannel correlator. The channel, in which the coefficient of reciprocal correlation between the excitation vector and communication vector reaches a maximum, becomes the indicator of the isolated signal parameter. The coefficient of correlation equals the cosine of the angle between the excitation vector and communication vector of a given detector. When the vector of excitation and vector of communications are collinear, the angle between them equals zero, whereas the cosine of the angle between vectors and coefficient of correlation equal 1. This means that this channel records the presence of the signal.

In Figure 6, angle ϕ between the initial excitation vector and communication vector of a given secondary detector is plotted on the x-axis. The family of curves characterizes the properties of secondary detectors adjusted for different values of input signal.

We should call attention to another distinction of construction of secondary detectors. As previously shown, the characteristic of primary detectors in the space of solitary vectors is described by a cosine curve, the value of which may be positive at some levels of stimulus and negative at others. However, in biological systems, one cannot transmit both positive and negative values over the same channel, since the only form of signal transmission over rather large distances in the nervous system is impulse frequency, whereas the coefficients of synaptic communication between neurons retain their sign. Thus, a special channel is required to transmit signals in the negative half-period of the cosine curve (Figure 7). In other words, the positive and negative parts of the characteristic of primary detectors are in different channels. For this reason, to execute the positive and negative parts of the characteristic of one primary detector we must have two separate primary detectors, each of which realizes only half the period of the cosine curve. As a result of such separation of "positive" and "negative" channels, the number of primary detectors is doubled.

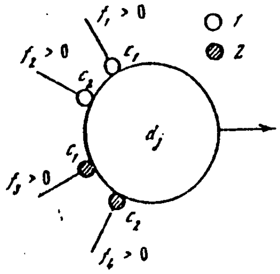

Figure 7.
Structure of detector with four inputs
1) excitatory 2) inhibitory

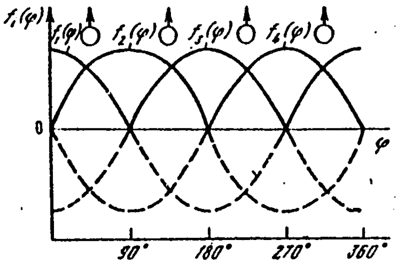

Figure 8.
Characteristic of primary detector with four inputs

The four inputs of the secondary detector are intended for transmission of only positive signals. With a change in the exogenous signal, instead of a change in sign there is a change in number of primary detector as input of the secondary detector. Alternation of signals is determined by the signs of the sine and cosine for different angles of the excitation vector. Positive signals come to the first and second inputs, while negative ones go to the third and fourth. This arrangement of the secondary detector is related to the fact that only impulses are transmitted in the nervous system, and the sign of synaptic communication of a given synapse remains constant. In order to impart another sign to the signal we need a separate channel. The dimensionality of the space of excitation vectors does not change.

In Figure 8, angle ϕ of the turn of the excitation vector representing a change in signal to the input is plotted on the x-axis, and the value of components of the excitation vector at each of the inputs is plotted on the y-axis. With a change in sign of excitation another primary detector is turned on:

$$f_1^*(\varphi)=\begin{cases} f_1(\varphi), & \text{if } -90^\circ \leqslant \varphi \leqslant 90^\circ; \\ f_3(\varphi) - & \text{in other cases} \end{cases}$$

and

$$f_2^*(\varphi)=\begin{cases} f_2(\varphi), & \text{if } 0^\circ \leqslant \varphi \leqslant 180^\circ; \\ f_4(\varphi) - & \text{in other cases.} \end{cases}$$

Only positive signals go from underlying elements to the secondary detector, which codes the signal parameter by channel number, if there is a double number of primary detectors. This is not associated with any change in excitation profile of secondary detectors (Appendix 1).

Model of analyzer. The aggregate of receptors, primary and secondary detectors forms the model of the analyzer of a specified signal parameter. At the first stage, the exogenous stimulus is coded with the set of excitations of receptors (or primary detectors that follow them) with characteristics in the form of a cosine curve. The positive and negative phases of the signal are transmitted over different channels. The set of excitations of primary detectors determines the direction of the excitation vector.

At the second stage, the excitation vector of primary detectors will create maximum excitation on one of the secondary detectors. The operation of scalar multiplication of the excitation vector by the communication vector is performed by means of the secondary detector. This determines the coefficient of correlation, and the signal is coded with the number of the most excited channel.

This analyzer model is close to the concept of biological analyzer advanced by I. P. Pavlov.

In the analyzer model, the difference in physical parameters of a signal is recoded into the difference in localization of excitation maximum on a set of detectors. We are impressed by the resemblance between the set of secondary detectors, on which the exogenous signal is reflected, and a receptive surface, for example, skin surface. As the stimulus shifts over the skin surface, the excitation maximum shifts from one receptor to another. In the detector model of an analyzer, with change in the stimulus there is a change in correlation between stimuli in receptors or primary sensory neurons, as a result of which the excitation maximum shifts from one output detector to another. The aggregate of secondary detectors, which form a sort of "brain screen" on which the change in a stimulus is reflected, could be called a quasireceptive surface. With change in signal properties, the excitation maximum shifts over such a quasireceptive surface, just like excitation shifts over a surface formed by receptors.

One can test the model for coding a signal by channel number in both psychophysical and neurophysiological experiments.

According to the detector model, different subjective sensations are represented by points on a n-dimensional sphere. The shortest distance between points on the sphere determines the subjective distance between corresponding stimuli: the smaller the difference between stimuli, the shorter the distance between points on the sphere that correspond to them. The dimensionality of the space found from analysis of psychophysical data must correspond to the number of primary detectors. Moreover, if an orthonormal basis is given in the perceptive space, the coordinates of the point as a function of value of the coded parameter should determine the characteristics of primary detectors in this space. If we know the function of sensitivity of primary detectors we can also calculate the sensitivity function of secondary detectors. This means that, on the basis of the principle of signal coding by channel number, we can turn from psychophysical data to the characteristics of individual detector neurons. In turn, we can obtain the characteristics of detectors independently, through electrophysiological experiments, using the same set of stimuli as in the psychophysical experiment.

Thus, the detector characteristics calculated on the basis of the model can be checked twice: first by analyzing the psychophysical data and then by directly examining the characteristics of neurons. The artificial analyzer constructed on the principle of signal coding by channel number, which consists of neuron-like elements with characteristics analogous to those of human detector neurons, makes it possible to create an internal representation of signals in a robot that would be analogous to the internal representation of signals in man. Then, the functions of signal discrimination by a robot will coincide with human functions of discrimination of these signals. In addition, by using the principle of signal coding by channel number, it is possible to create artificial sense organs for a robot that do not exist in man. This can be achieved by using sensors that are wanting in the set of human receptors, as well as combinations of receptors that are not inherent in man. With some combination of receptors, the dimensionality of the perceptive space of a robot may differ from the dimensionality of the human perceptive space. Although this would disrupt the coincidence of internal conception [representation] of signals in man and robot, the similarity of principles of constructing sensory systems facilitates the recoding problem when organizing communication between man and robot.

Problems of enhancing analyzer sensitivity. Under the influence of a stimulus on an analyzer, an excitation vector arises in its receptors or primary detectors beyond the receptors, which affects immediately the entire population of secondary detectors through the fan of communication vectors. Each communication vector is specific to a given secondary detector. As a result, an excitation profile is generated on the population of output detectors in the form of distribution of excitations on secondary detectors with a solitary maximum on one of them. With change in the stimulus, the excitation vector formed by primary detectors changes, and the excitation maximum shifts from one secondary detector to another.

The degree of difference between one stimulus and another is determined by the angle between the excitation vectors that they induce, or length of the arc that separates the secondary detectors that represent these stimuli on the sphere.

The discrimination threshold is determined by the distance between adjacent secondary detectors. Thus, the precision of analyzer function is determined by the density of output detectors represented by points on an n-dimensional sphere and forming a quasirecepitve surface. With a set density of detectors on the quasireceptive surface, the precision of analyzer function depends on the level of the excitation maximum in the detector population (on selectivity of the excitation profile), on the one hand, and on the angle of rotation of the excitation vector with change in stimulus, on the other. The capacity to distinguish between stimuli depends both on the speed of rotation of the excitation vector with change in stimulus and on the precision, with which the analyzer can measure different directions of the excitation vector. Thus, the problem of enhancing differential sensitivity of the analyzer can be reduced to two different problems: increasing precision of measurement of direction of excitation vectors (or increasing selectivity of the multichannel correlator) and increasing the speed of rotation of the excitation vector with change in stimulus.

The problem of increasing accuracy of measuring the direction of the excitation vector with a given number of secondary detectors amounts to increasing selectivity of the excitation profile on the population of secondary detectors (i.e., the problem of increasing level of excitation maximum). Lateral inhibition between secondary detectors, which is analogous to lateral inhibition between eccentric cells of the Xiphosura eye, is the mechanism that increases acuity of the excitation profile. This lateral inhibition implies that there are inhibitory connections between all output detectors. The value of the coefficient of these inhibitory relations decreases with increase in distance between detectors.

Considering the reciprocal inhibition of secondary detectors, the reaction of a given detector equals the influence from primary detectors minus overall inhibition from the outputs of all secondary detectors, with the exception of that one. The inhibitory communications of this detector with all other detectors, with the exception of its communication with itself, form the components of the communication vector of lateral inhibition. All excitations of secondary detectors, with the exception of the given one, constitute components of the supplemental excitation vector. The reaction of the secondary detector with consideration of lateral inhibition can be expressed in vector form. The reaction of this secondary detector, with consideration of lateral inhibition, equals its initial excitation minus the scalar product of the vector of lateral connections multiplied by the supplemental excitation vector. When the output detector has two inputs (two-dimensional case) and the n-dimensional sphere degenerates into a circumference, it is convenient to describe the excitation profile in polar coordinates. For this purpose, one should plot the value of excitation of the secondary detector on each communication vector characterizing this detector. Let us call such a description of the excitation profile the diagram of orientation of the detector system. As a result of lateral inhibition the number of the detector with maximum excitation does not change. However, the acuity of the excitation profile increases and so does the excitation maximum on a set of detectors. Figure 9 illustrates the change in the digram of orientation [direction] of the detector system with and without consideration of lateral inhibition.

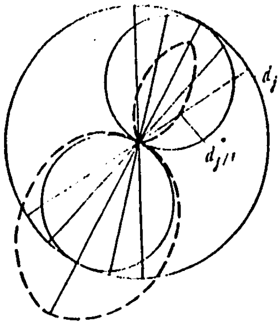

Figure 9.
Change in orientation diagram under the influence of lateral inhibition

The circumference is formed by the fan of secondary detector communication vectors $|C_j|$ = const. The solid line shows responses of secondary detectors that form the excitation profile in a set of detectors when there is no lateral inhibition: $d_{j/i} = (C_j, F_i)$. With introduction of lateral inhibition, the level thereof k_{ij} shows which share of the signal from the output of the jth secondary detector enters the input of the ith detector. The responses of secondary detectors diminish by a value that equals the sum of products of coefficients of lateral communications multiplied by the corresponding excitation of adjacent detectors:

$$d^*_{j/i} = d_{j/i} - \sum_{j=1}^{n} k_{jl} d^*_{l}$$

where $1/k_{jl} = r \arccos (C_l, C_j)$ (r = const), the coefficient of lateral relation is inversely proportional to the distance between secondary detectors or angle between communication vectors that represent them (dash line).

The directional diagram undergoes no change in orientation as a result of lateral inhibition, but it becomes narrower and receives additional inhibition: its inhibitory path increases.

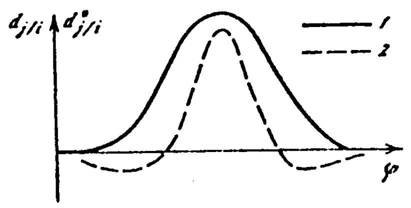

Figure 10.
Sharpening of excitation profile of a set of secondary detectors under the influence of lateral inhibition

1) magnitude of reaction $d_{j/i}$ of jth secondary detector under the influence of ith stimulus
2) reaction of the same detector, but with consideration of lateral inhibition, i.e., value of $d^*_{j/i}$ (see Figure 9)

The same can be described in a rectangular system of coordinates; for this, the angle characterizing the direction of the communication vector is plotted on the x-axis and the level of excitation of the corresponding detector on the y-axis. Under the influence of lateral inhibition (Figure 10), the excitation profile becomes more selective, and an additional flanking zone of inhibition appears on it. There is no change in position of excitation maximum on the x-axis. Angle ϕ characterizes the inclination of the communication vector of each secondary detector. Lateral inhibition lags in relation to excitation. For this reason, there is gradual development of increase in selectivity of the excitation profile on the set of the detectors under the influence of a stimulus. Since lateral inhibition has a threshold, acuity of the excitation profile does not increase with low signal intensities. As a result, lateral inhibition turns off and analyzer sensitivity diminishes when signal intensity is lowered.

Adaptation of primary detectors as a means of enhancing differential sensitivity in the vicinity of an adaptive stimulus. When observing a stimulus for a long time it becomes necessary to detect the slightest deviations of its parameters. In a spherical model, the threshold of differential sensitivity is measured by the value by which the stimulus parameter must be altered so that the excitation maximum would shift from a given detector to another one that is closest to it. The higher the detector density on a quasireceptive surface, the lower the threshold. However, increasing detector density alone will not yield the desired increase in analyzer sensitivity. Indeed, if the number of output detectors is large enough, there will be an insignificant difference between the activity of two adjacent neurons. If, however, we take into consideration noise, under its influence the excitation maximum with a constant stimulus will wander around a certain detector over the quasireceptive surface, and for this reason the accuracy of determining the stimulus parameter will not improve. One cannot improve accuracy of stimulus perception by only increasing the number of secondary detectors, without lowering the noise level.

However, one can solve the problem of improving sensitivity in another way [14, 15]. With a given density of secondary detectors, the sensitivity of the system to change in stimulus parameter is determined by the angle of rotation of the excitation vector. In order to improve sensitivity of the system to a change in parameter of a long-lasting stimulus (which we shall call the adaptive stimulus hereafter), we must find a means of increasing the rotation of the excitation vector when the adaptive stimulus changes. This means must provide for a change in characteristics of primary detectors under the influence of adaptive stimulus that would increase the rotation of the excitation vector with change in active stimulus. The initial characteristics of primary detectors are such that they provide for attainment of maximum sensitivity by the entire analyzer. For this reason, modification of characteristics of primary detectors by the adaptive stimulus cannot lead to overall increase in sensitivity of the system. Concurrent decrease is observed in sensitivity in relation to other signal parameters with increase in system sensitivity to a change in the adaptive stimulus. One can obtain a temporary change in analyzer sensitivity in the vicinity of the active stimulus by modifying the characteristics of primary detectors as a result of adaptation. It is assumed that sensitivity of primary detectors diminishes proportionally to their excitation with prolonged exposure to an adaptive stimulus. The components of the excitation stimulus with the highest absolute value decrease the most, whereas those close to zero decrease insignificantly. As a result, there is approximation of components of the excitation vector. This is illustrated in Figure 11, where angle ϕ characterizes the direction of the excitation vector. Such equalization of components of the excitation vector, attributable to the different change in level of excitation of primary detectors, leads to a change in direction of excitation vector during adaptation. This leads to a change in the number of output detector with maximum excitation, which is perceived as a change in the active stimulus (Figure 12). Selective secondary detectors are represented by the small circles on the circumference. The position of the secondary detector with maximum excitation is determined by the correlation between components of the excitation vector of primary detectors. Before the start of adaptation, the excitation vector occupies a position in which its components differ markedly from one another. After adaptation, the strongly excited primary detector changes more than a mildly excited one; the components of excitation vector F* will differ less and the vector will turn in the direction of a 45° angle (dash line).

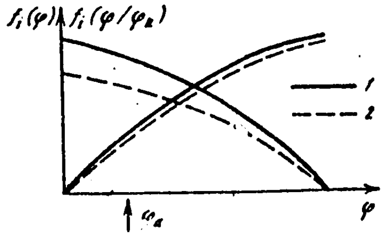

Figure 11.
Adaptation of primary detectors

1) components of excitation vector of primary detectors before adaptation $F_i(\phi)$
2) components of excitation vector after adaptation $F_i(\phi/\phi)$

(value of adaptive stimulus shown by arrow)

As a result of adaptation the excitation vector of primary detectors strives to occupy a position where its components equal one another. The excitation vectors whose base elements are equal, as well as those

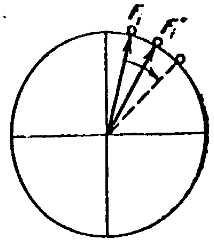

Figure 12.
Rotation of excitation vector after adaptation in the primary detector element

with only one component other than zero, do not change their direction during adaptation. The last excitation vectors, whose second component equals zero, coincide with the direction of one of the basis vectors (Appendix 1).

The degree of subjective change in a stimulus under the influence of adaptation of primary detectors is measured by the angle of rotation of the excitation vector in relation to its initial position. The profile of excitation generated on the population of secondary detectors turns by the same angle as the excitation vector (Figure 13). The magnitude of reaction of a given secondary detector is plotted along the vector radius. The excitation maximum shifted to another secondary detector under the influence of adaptation, which corresponds to a change in perception of this signal. The direction of the excitation vector whose components are equal will not change under the influence of adaptation. The position of the excitation profile on the population of secondary detectors will not change either. For this reason, the stimulus that generates an excitation vector with equal components will emerge as the limit toward which all other stimuli will strive. The only exceptions are stimuli corresponding to basis vectors. It can be stated that such a stimulus emerges as a certain norm. When a stimulus comes close to such a norm as a result of development of adaptation it is generally called normalization.

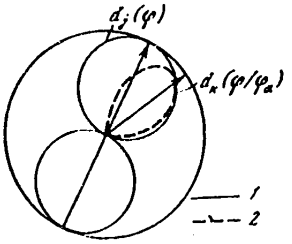

Figure 13.
Shift of excitation profile of secondary detectors under the influence of adaptation of primary detectors
1) profile of excitation before adaptation
2) after adaptation

The process of adaptation of primary detectors develops gradually, with some inertia. For this reason, all of the adaptation effects depend on duration of the stimulus and time that elapses after it is discontinued.

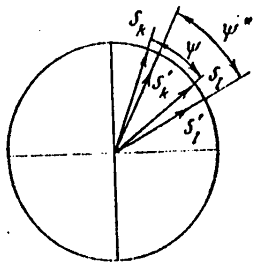

Figure 14.
Increased discriminating sensitivity in the vicinity of an adaptive stimulus

It should be noted that all changes in sensitivity of primary detectors elicited by the adaptive stimulus will persist for some time after it is discontinued. For this reason, a stimulus delivered after an adaptive one will elicit excitation of primary detectors to a different level than a stimulus delivered when there is no adaptation. In other words, a stimulus delivered prior to preliminary adaptation and after development of adaptation generates, in the general case, excitation vectors that differ in direction. Thus, the same stimulus elicits maximum excitation of different secondary detectors before adaptation and after adaptation, and for this reason is perceived as two different stimuli. This effect is called the aftereffect. An adaptive stimulus alters the most markedly the excitation vector in relation to itself and similar stimuli. Two similar [or close] stimuli in the vicinity of the adaptive stimulus would differ more after adaptation than before. This is attributable to the fact that the greater the initial excitation of components of the excitation vector, the more they diminish as a result of adaptation (Figure 14). Two excitation vectors F_k and F_l are shown in polar coordinates, which are generated by two different stimuli, S_k and S_l. The angle between these excitation vectors before adaptation equals arc ψ between the ends of these vectors. Under the influence of adaptation, the characteristics of primary detectors changed in such a way that the angle between the new excitation vectors F_k and F_l increased and became ψ^*. This means that the subjective distance between stimuli S'_k and S'_l increased as a result of adaptation: $\psi^* > \psi$. This increase in subjective distance occurs only in the vicinity of the adaptive stimulus. There may be poorer discrimination of stimuli other than the adaptive one after adaptation.

Thus, differential sensitivity of the sensory analyzer increases locally under the influence of adaptation (Figure 15). In this figure, the value of angle $\Delta\phi$, which characterizes the direction of the excitation vector is plotted on the x-axis and the change in subjective distance between stimuli, $\Delta\psi = (F(\phi + \tau/\phi_a), F(\phi/\phi_a)) - (F(\phi + \tau), F(\phi))$, $\phi_a = 2\Delta\phi$.

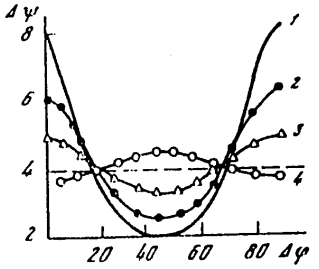

Figure 15.
Effect of adaptation on discriminating sensitivity of two-dimensional model

1) $\phi_a = 0$
2) $\phi_a = 22°30'$
3) $\phi_a = 37°30'$
4) $\phi_a = 45°$

Illusions of perception--normalization and aftereffect--are the cost of enhanced sensitivity. Introduction of adaptation into primary detectors of artificial sense organs of the robot elicits a gain due to an improvement of their capacity for signal discrimination. This brings even closer the sensory system of man and robot: human and robot perception illusions also become the same.

In conclusion, it must be noted that, in addition to adaptation of primary detectors, one must consider adaptation of secondary detectors, which is manifested by a decrease in sensitivity proportionately to the degree of their excitation. As a result of such a decrease in sensitivity of secondary detectors there is an increase in absolute threshold of perception for stimuli that are close to the adaptive one. This influence has an aftereffect: in order to detect the adaptive signal its intensity must be increased, even after some time has elapsed.

Adaptation at input of primary detectors as a means of augmenting the dynamic range of analyzer operation. Differential sensitivity in relation to successively delivered stimuli is increased by increasing the angle between excitation vectors. In this case, the vector modulus is not taken into consideration. It is assumed that the intensity of the signal does not affect evaluation of its other parameters. The limitations of this assumption are obvious, at least for low intensities. If the stimulus is so weak that it cannot elicit excitation in a receptor, it is impossible to perceive it.

Moreover, one must consider the fact that a stimulus usually appears against a certain background. If this background is not suppressed, the components of the excitation vector will not differ from another, and it will be impossible to distinguish signals.

The receptors must be sensitive to both low stimulus intensities and the slightest changes in signal intensity in relation to the background for the analyzer to function effectively. Consequently, there must be a combination in the analyzer of a wide dynamic range and significant characteristic slope. A special mechanism must be added, that would maintain receptor sensitivity to changes in the useful signal, to broaden the dynamic range of the analyzer without lowering differential sensitivity. For this, the working point of the receptor characteristic must remain in the steepest segment. The purpose of this mechanism is to limit the intensity of the stimulus affecting the receptor. The amplitude characteristic of the receptor shifts along the axis of signal intensity by a distance that is determined by intensity of the background. The working point of the receptor always remains at the steepest part of its characteristic (Figure 16). The input signal of primary detectors is cut off by adjusting the threshold of the receptor--primary detector connection. The threshold is adjusted by H elements, the degree of excitation of which depends on receptor excitation.

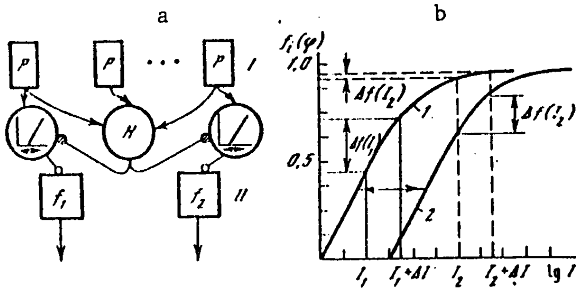

Figure 16. Adaptation at primary detector input

a) adjustment of sensitivity of primary detectors under the influence of the background (I--layer of receptors, II--layer of primary detectors)
b) shift of amplitude response of primary detector as a function of intensity of stimulus to receptors

The intensity of the stimulus is plotted on the x-axis and amplitude of detector response with different background intensities is plotted on the y-axis. I_1, I_2 are current value of background intensity, while ΔI is increment of signal intensity in relation to the background. If there is no regulatory mechanism, the response of the primary detector is fixed (curve 1). In this case, the detector's reactions to background I_2 and stimulus $I_2+\Delta I$ will almost coincide. If the mechanism of threshold regulation is turned on, the detector's response will shift along the x-axis (curve 2) and the reaction of the same detector to background I_2 and stimulus with intensity $I_2+\Delta I$ will be different. Regulation of the threshold provides for automatic shift of the response [characteristic] in such a way that a deviation from the background will elicit a strong change in the reaction of the primary detector.

Such a mechanism can be introduced either on the receptor level or at the point of communication between receptors and primary detectors.

Interaction between elements of analyzer field as a means of enhancing sensitivity. Another task that often has to be done under real conditions is to compare two simultaneously delivered stimuli according to some parameter and determine whether they are equal or not. Heretofore, we have discussed only one local analyzer consisting of a set of receptors linked to output detectors either directly or through primary detectors. The characteristics of primary detectors are described by a cosine curve. When a stimulus is delivered to a population of output detectors an excitation vector is activated, which creates maximum excitation on one of them. If the stimulus changes, the excitation maximum shifts over the set of output detectors represented by points on an n-dimensional sphere. The signal is analyzed in relation to the local segment of space. Numerous local analyzers of the same type form a field that is affected by several stimuli. Each stimulus is analyzed by its own local analyzer; however, there could be considerable overlapping of areas of action of local analyzers.

The problem of equality of two stimuli delivered to different local analyzers can be solved by determining whether these stimuli elicit in each of the local analyzers maximum excitation of detectors bearing the same number. If both stimuli excite to a maximum degree secondary detectors with the same numbers, it is decided that the stimuli are equal, otherwise the stimuli are perceived as being different. The degree of difference between stimuli is determined by the angle between excitation vectors in each of the local analyzers.

If the local analyzers function independently of one another, the problem of improving accuracy of assessing stimuli amounts to increasing the number of secondary detectors in each of them. However, the problem cannot be solved by unlimited increase in number of secondary detectors.

The question arises as to how to improve the effectiveness of signal discrimination by a set of local analyzers. Let us consider two local analyzers corresponding to two different sections of the field in which the signals operate. Let a stimulus be delivered to one section that generates an excitation vector in one analyzer. The other stimulus generates an excitation vector in the adjacent section. If we now introduce lateral inhibition between analogous primary detectors of different local analyzers, the angle between excitation vectors generated in different sections of the field will increase.

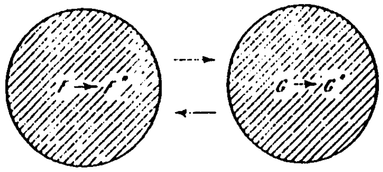

Figure 17.
Diagram of interaction between two local analyzers

The arrows in Figure 17 show the action of two stimuli S_k and S_l on receptive fields of two adjacent analyzers. The receptive fields of local analyzers are shown by the striped regions. Each stimulus generates its own excitation vector F and G in the local analyzer. The exitation vectors are modified and diverge (vectors F* and G*) under the influence of lateral inhibition of analogous detectors.

Figure 18 illustrates divergence of excitation vectors. Two stimuli elicit different excitation vectors F and G in two local analyzers. The components of the excitation vector change (F* and G*) under the influence of lateral inhibition between analogous detectors in such a way that the angle between points representing the signals increase: $\psi^* > \psi$. This means that the subjective distance between stimuli

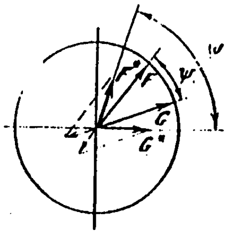

Figure 18.
Divergence of excitation vectors under the influence of lateral inhibition between analogous primary detectors

increased. The excitation vectors of two identical stimuli retain their position with such interaction. Subjectively, these stimuli are perceived without changes. At the bottom of the figure we see that vector $F^* = F - \alpha G$ and $G^* = G - \alpha F$. This means that the form of lateral inhibition discussed enhances differential sensitivity of the entire system. Different signals shown in spatially different regions can be distinguished more effectively. At the same time, if two stimuli generate identical excitation vectors in two different sections of the field, with introduction of lateral inhibition the signals are perceived as identical, just the same as without lateral interaction.

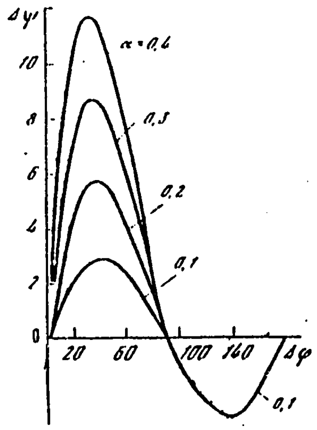

Figure 19.
Magnitude of simultaneous contrast as a function of force of lateral inhibition between analogous primary detectors

With increase in objective difference between stimuli, there is an increase in the angle between excitation vectors and the degree of subjective difference between them increases. If two stimuli generate excitation vectors in opposite directions, interaction between analyzers does not alter subjetive evaluation of the stimuli. If subjective distance between stimuli is at a maximum, lateral inhibition does not alter orientation of vectors of excitation and does not increase the subjective difference between them (Figure 19). The angle between excitation vectors corresponding to interacting stimuli $\Delta\phi = \phi/2$ is plotted on the x-axis, and changes in subjective distance between stimuli $\Delta\psi = F^*(\phi_1)$, $G^*(\phi_2) - F(\phi_1)$, $G(\phi_2)$ are plotted on the y-axis (see Figure 18); α is the value of the coefficient of lateral inhibition. Negative values were omitted in the right part of the graph.

If lateral inhibition between analogous primary detectors of different local analyzers is increased, maximum increase in subjective differentiation between two stimuli is obtained with smaller objective differences between them.

The excitation vectors diverge under the influence of lateral inhibition between analogous primary detectors of different loci by an angle that is wider than the angle characterizing subjective differences between stimuli in the case where lateral inhibition is absent. Consequently, lateral inhibition between analogous primary detectors emphasizes the differences between stimuli. This is obtained without increasing the number of output detectors. Concurrent contrast and concomitant perception illusions are the cost of this gain in differential sensitivity.

It is important to stress that simultaneous contrast is a universal effect, and it could be manifested in all types of sensory systems where there is a set of identical analyzers that function concurrently, which have primary detectors linked by reciprocal inhibition. The magnitude of simultaneous contrast depends on the objective difference between stimuli. Identical stimuli or those that are at a maximum distance in subjective space do not elicit simultaneous contrast. Moreover, the closer the stimuli are to one another in the receptor field, the greater the simultaneous contrast. The inertia of lateral inhibition explains simultaneous contrast as a function of time. Since lateral inhibition induced by a stimulus can persist for some time after discontinuing stimulation, it is capable of depressing milder excitation in adjacent regions. This leads to masking of one stimulus by another that is spatially close to it. The masking effect is at a maximum for stimuli that generate identical excitation vectors in adjacent regions. The masking effect also depends on intensity. A stronger stimulus raises the excitation threshold for analogous stimuli in adjacent regions, masking adjacent stimuli.

Invariant detector. The most important distinction of human and animal perception is its constancy. Thus, even though the image shifts from some retinal elements to others with eye movement, the object is perceived in a stable way, in accordance with its constancy in the environment. The robot's internal conceptions must also have constancy, analogous to that of human perception. To provide constancy of visual perception, information is needed about the position of the eyes, either in the form of feedback from proprioceptor muscles of the eyes, or in the form of copies of commands given to control eye movement. The neuronal mechanism of constancy of perception is universal for all analyzers, and it is related to the concept of invariant detector. While it was previously believed that secondary detectors of a local analyzer have a constant set of relations with primary detectors, the links between an invariant detector and detectors on a lower level change in accordance with signals coming from other analyzers. These signals perform a controlling function, modifying the communication vector by which the invariant detector is linked to the set of underlying detectors (Figure 20). The invariant detector is characterized by a communication vector $(g_1, g_2, \ldots, g_5, \ldots)$ that is collinear with the vector of excitation of the additional set of detectors. When the excitation profile of the additional set of detectors changes, so does the communication vector. The arrows show that the coefficients of communication between aconstant and invariant detectors acquires values of $m_1, \ldots, m, \ldots$ under the influence of stimulation of detectors of the additional set. If there is simultaneous change in excitation vector F and control vector of excitation $M = \{m_1, \ldots, m_5, \ldots\}$, the level of excitation of invariant detectors remains constant, and the location of excitation maximum on the set of invariant detectors does not change either. If only the control vector changes with a constant signal at the input, there is the illusion of change in the stimulus. This happens because the communication vector changes, and this causes a shift of excitation maximum from one invariant detector to another.

Thus, we can distinguish two sensory signals: the main one going to the invariant detector and an additional one, which modifies the communication system of the invariant detector with the underlying level. The modifying signal depends on which stimulus is delivered to the input of the additional system of detectors. This stimulus determines the channel in which signals from underlying detectors will create maximum excitation. With a change in signal at the input of the additional detectors, there is also a change in the number of the invariant detector with maximum excitation.

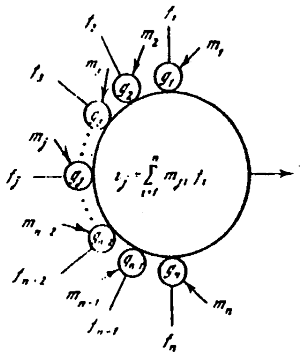

Figure 20.
Diagram of invariant detector

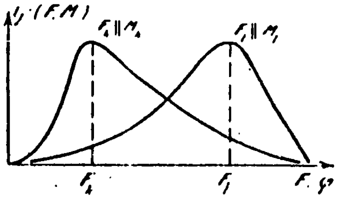

Figure 21.
Change in characteristic of invariant detector under the influence of a controlling vector that modifies the communication vectors

The functional role of the additional analyzer is to determine the magnitude of change in distribution of stimuli on a set of invariant detectors, as compared to their distribution on a set of aconstant detectors (Figure 21).

In Figure 21, a stimulus represented by an excitation vector or angle that gives it is plotted on the x-axis and the scalar product $i = (F, M)$ of the excitation vector multiplied by the communication vector of this invariant detector with two different values for control vector M_k and M_l is plotted on the y-axis. This figure illustrates a two-dimensional case. With one controlling vector the invariant detector is adjusted for one signal; with a change in controlling vector, when the communication vector changes, the same invariant detector becomes selectively adjusted for the other signal. The invariant detector responds with a maximum reaction to the signal whose excitation vector is collinear to the formed communication vector.

Thus, the vector controlling the additional set of detectors changes the communications of invariant detectors in such a way that with a shift of the maximum for the set of additional detectors the excitation maximum created in the main set of detectors shifts over the set of invariant detectors. The effect of constant perception arises when the shift of excitation maximum over the set of additional detectors is associated with a shift of excitation maximum over the main set as well. The control vector, which alters the communications between aconstant and invariant detectors, creates an excitation maximum on the same invariant detector. Thus, when the eyes are turned, the image shifts over the retina; however, the controlling vector generated by the analyzer of viewing direction changes the communications between aconstant and invariant detectors in such a way that the image is retained on the same invariant detectors all of the time. This is what provides constancy of visual perception of direction during eye movement.

Constancy of perception in the model under discussion amounts to the following. There are at least two sets of detectors. Some detectors perform the function of main ones that perform analysis of stimulus parameters, the second is the set of additional, ancillary detectors. The signals they contain alter the communications between the main and invariant detectors forming the set of output detectors. When there is coordinated shifting of excitation maximums over the main and additional sets of detectors, distribution of stimuli on the set of invariant detectors does not change. The set [or numerous] of invariant detectors forms the internal screen that permits constant reflection of the outside world with coordinated change in positions of excitation maximums on the main and ancillary set of detectors. The mechanism that provides for invariance of perception is of great adaptive significance; however, it generates illusions of perception. Thus, if there is no change in the signal on the set of main detectors but the excitation maximum shifts over the set of additional detectors, the distribution of stimuli on the set of invariant detectors will shift constantly, in accordance with changes in the controlling vector. As a result, there is the illusion of change in stimulus. The sensation of movement of an image that is stabilized in relation to the retina during eye movement is an example of such an illusion.

Mixture effects in the analyzer coding signal parameters by channel numbers. An input signal acting on receptors elicits a reaction by primary detectors, which determines the value [significance] of components of an n-dimensional excitation vector. If a second stimulus is delivered simultaneously to the same receptors, the level of excitation of primary detectors is determined by the sum of the effects of these two stimuli. Formally, the joint effect of stimuli is determined by the sum of the two excitation vectors generated by these stimuli. The components of the resultant excitation vector equal the sum of corresponding components of the initial vectors. In the general case, the direction of the resultant excitation vector differs from the direction of each of the initial vectors, i.e., the position of the excitation maximum on the set of output detectors under the simultaneous effect of two stimuli differs from the position of excitation maximum when only one of them is delivered (Figure 22). In other words, concurrent delivery of two stimuli to the input of a local analyzer elicits a different subjective sensation than each of the summated stimuli separately. Let a stimulus generate an excitation vector that is collinear with the vector generated by two simultaneously delivered stimuli; then such a stimulus cannot be distinguished from the sum of the two stimuli. Thus, coding by channel number leads to formulation of a generalized law of mixture of stimuli, a special instance of which is the well-known law of mixture of odors, gustatory sensations and colors. The law of mixture [confusion?] applies in the analyzer of line slant, analyzer of depth [16] and analyzer of motion.

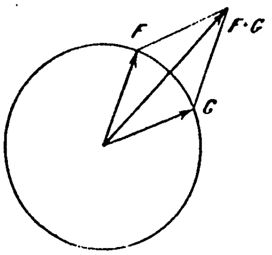

Figure 22.
Mixture of two simultaneously acting stimuli (F and G--initial excitation vectors; vector F+G is the sum of vectors F and G)

If the components of the excitation vector of one stimulus are equal, but components of the excitation vector of the other stimulus are of the opposite sign, together they will yield a zero vector with components equaling zero, i.e., there will be mutual depression of signals in the system. Such an effect is observed when certain odors are mixed.

If the sensitivity characteristics of primary detectors are known, the effects of stimulus mixing can be predicted. The study of the law of signal mixing makes it possible to indirectly estimate the number of independent signal receivers and, in a number of cases, to find unknown characteristics of primary detectors.

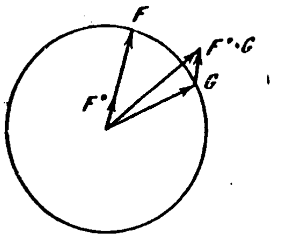

Figure 23.
Mixing of two successive signals

Considering the inertia of excitatory and inhibitory processes in real neuronal networks, one could expect mixing effects with successive delivery of two stimuli to the input of a local analyzer. Indeed, excitation of primary detectors induced by a stimulus diminishes gradually after it is discontinued. This means that, after a stimulus is discontinued, the excitation vector it generated also disappears gradually, with some lag. If a second stimulus is delivered after discontinuing the first one, perception is determined by the sum of excitation vectors of the preceding and next stimuli, with consideration of the dynamics of their reaction (Figure 23).

Residual excitation persists for some time after the stimulus on the level of primary detectors, and this determines vector F*. If a second stimulus is now delivered, its excitation vector G is added to the vector of residual excitation F*. The new excitation vector G+F* determines perception that differs from perception of the first and second signals delivered separately, as well as from the sum thereof, when they are used simultaneously. The contribution of the fading trace of the excitation vector to the overall excitation vector diminishes with increase in interval between stimuli.

Command neuron. In developing artificial sense organs for a robot, which are based on the principle of signal coding by channel number, the question arises as to how to coordinate such a multichannel, parallel-operating analyzer system that has an hierarchic structure with the actuating performance of the robot. This question requires special consideration. In this work, coordination of the principle of signal coding by channel number with actuating functions is obtained by following the biological prototype. The pricniple of coding by channel number extends to realization of reactions. This is related to the concept of command neuron. The command neuron is a structure that is analogous to a detector, but with an inverted communication tree. If the detector responds with maximum excitation to a specific combination of signals delivered to it over several channels with different coefficients of amplification, the command neuron that is excited forms a controlling vector due to the different coefficients of communication with underlying neurons. There is a solitary combination of effectors, which emerges as a specific reaction of the organism in analysis of behavior, that corresponds to this controlling vector. In the simplest case, the components of the control vector are excitations from the command neuron which pass through motoneurons to the input of effector elements. Figure 24 illustrates the structure of a command neuron. Signals $(d_1, d_2, \ldots, d_4, \ldots)$ from different detectors come to the input of the command neuron through synaptic connections characterized by coefficients of communication $(q_1, q_2, q_3, \ldots)$. Excitation going from the command neuron through connections $\{w_1, w_2, w_3, \ldots\}$, triggers a reaction through a set of motoneurons that create control excitation vector R_j, which creates a certain pattern of effector responses, and this determines the output reaction. With reference to the correlation between components of the control vector generated by a given command neuron, one must also take into consideration the time of propagation of impulses over communications with "actuating [effector] mechanisms." The time "pattern" of synaptic effects on the effector inputs may also be of substantial significance.

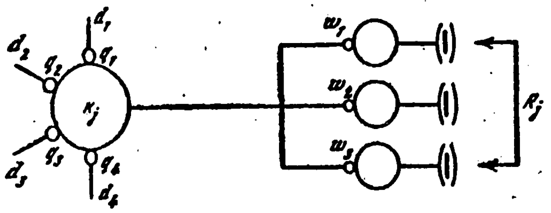

Figure 24. Structure of command neuron

The diversity of command neurons generating different control vectors can create a wide diversity of fixed reactions with a limited set of effector elements.

Thus, if an exogenous signal generates in a sensory system an excitation vector that creates maximum excitation on one of the secondary detectors, the excitation of one command neuron generates a control vector whose components are the product of magnitude of excitation of the command neuron multiplied by the components of the vector of communication with underlying elements.

Excitation of one command neuron leads to a reaction or fragment of a reaction. Thus, in the simplest case, the list of command neurons corrresponds to the list of elementary reactions.

The diversity of elementary reactions is determined by the diversity of command neurons. By analogy with the hierarchic structure of detectors, we can conceive of the hierarchic system of command neurons which, due to complication of communications, generates an increasing diversity of reactions.

The choice of some reaction or other signifies excitation of some command neuron or other. In the simplest case, the choice of reaction consists of stimulating detectors through the exogenous environment which converge on the command neuron. A combination of detectors converging on a command neuron forms the specific stimulus for a given reaction. In ethology, such relations are described under the name of "lock and key."

If there is no change in time in the communication of the set of detectors with a given command neuron and it does not depend on number of signals delivered, nor is it a function of combining one signal with another, such a command neuron does not have flexibility. Flexible command neurons are those whose coefficients of communication with detectors change as a function of number of stimuli delivered or as a function of combination of signals at the input.

Field of command neurons. Each command neuron is characterized by a specific control vector that generates a specific reaction. The reactions of different command neurons may differ from one another in such a way that, together, they form a field of command neurons with a wide assortment of reactions. The system of command neurons involved in saccadic control of eye movement could be an example of such a field. Each command neuron implements movement of the eyes in a specific direction and over a specific distance. A set of such command neurons permits displacement of the eyes in relation to their initial position. This makes it possible to transfer the image of any object on the retina to the required position, for example, to its most sensitive part.

One can develop a technical system of organization of motion on this principle. For this, one should organize a set of analogues of command neurons that together form a field. The control vectors of these command neurons must overlap the given space. Reaching a specific point in space amounts, in this case, to the choice and excitation of a specific command neuron. The given trajectory of a complex movement is obtained by shifting the focus of excitation over the field of command neurons.

With the use of signals of invariant detectors as signals at the input of command neurons, one can organize a field of command neurons that implement reactions with consideration of constancy of signal perception.

Lateral inhibition between command neurons and change in priority of reactions. The command neurons of each level are connected to one another by lateral inhibition. Excitation of one command neuron inhibits all other command neurons. The uniqueness of choice is thus provided.

The choice of a reaction depends not only on which stimulus is involved, but which reaction is preferable in a given situation. For example, when an animal experiences great thirst it does not pay attention to food which, in another situation, would be far from indifferent.

The mechanism of change in priority of command neurons controlling reactions is involved in the choice of preferred reaction. This is achieved by means of special modulating neurons. The set of values that alter the excitation of each command neuron constitutes a modulating vector, which redistributes the priorities of command neurons and, consequently, reaction priorities. In combination with lateral inhibition between command neurons, the mechanism of redistribution of reaction priorities provides for a solitary choice of reaction in accordance with the requirements of the prevailing situation.

In each situation, in addition to situational signals, a modulating excitation vector is delivered to the set of command neurons, and it alters the priorities of command neurons. Modulating vectors are realized by modulating neurons, which receive signals from receptors of internal states: hunger, thirst, respiration, temperature. The actions that conform with a given situation are performed as a result of redistribution of priorities of command neurons.

Instruction as disconnection of detectors from a command neuron. In constructing a robot with consideration of interaction between detectors and command neurons, it is necessary to construct a system of communications from command neurons to motoneurons and effector elements after selecting a specific set of reactions. These communications are realized by the corresponding control vector which implements occurrence of the reaction. It is then necessary to select a vector of communication between the set of detectors and each of the command neurons that will determine the selectivity of calling for the reactions.

The robot can be instructed either by means of expanding the repertoire of reactions or changing their composition. This is achieved by including in the list of possible actions some additional reactions and excluding unnecessary reactions. This is done by changing the effectiveness of communication between command neurons and effector [actuating] elements. And it is necessary for these communications to be flexible.

If the alphabet of robot actions is constant, instruction amounts to transformation of communication between the detectors and command neurons. This could consist of disconnecting previously connected detectors, connecting previously disconnected detectors and combination of these processes. In this case, the communications between detectors and the command neuron must be flexible.

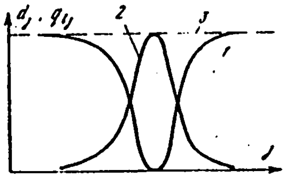

Figure 25.
Disconnection of detectors from command neuron
1) coefficients of communication the value of which is inversely proportional to the value of the detector excitation
2) profile of detector excitation
3) initial level of coefficients of communication between detectors and command neuron
j) detector No
d_j) level of its excitation
q_{li}) value of coefficient of communication of jth detector with lth command neuron

Let us consider instruction as disconnection of detectors from the command neuron. Let a set of detectors be connected to the command neuron. Upon delivery of a stimulus, a certain excitation profile passing to the input of command neurons is formed in this set of detectors. If we assume that the communication coefficients diminish proportionately to the degree of their excitation, with repeated delivery of the same stimulus the excitation going to the input of the command neuron becomes lower and lower from stimulus delivery to delivery, so that ultimately this command neuron ceases to react. The higher this process of adaptation in the system of primary and secondary detectors, the longer the extinction of the command neuron reaction lasts. Formally, extinction of the command neuron's reaction in the case of delivery of a stimulus many times can be interpreted as the result of formation of a new communication vector, the direction of which does not coincide with the direction of the initial communication vector between detectors and command neurons. Thereby, under the influence of a stable stimulus situation, the command neuron becomes selectively adjusted expressly to it. Adjustment is manifested by selective blocking of signals elicited by this stimulus. In turn, this leads to a situation where the stimulus no longer elicits the reaction that the command neuron in question controls (Figure 25).

With a change in stimulus, the excitation profile shifts over the set of sensory detectors, as a result of which there is no longer compensation by the transformed communication vector of excitation delivered to the input of the command neuron. Thus, the command neuron is a cut-off filter: it does not react if the signal coincides with a prior stimulus and it reacts when the preceding and subsequent stimuli do not coincide [17]. This situation is illustrated in Figure 26. The value of stimulus S is plotted on the x-axis and the reaction of the command neuron k_j, which equals the product of the vector of transformed communications multiplied by the excitation vector D generated by a signal in secondary detectors, is plotted on the y-axis. The vertical dotted line shows the position of the stimulus that was used during instruction S_0. After instruction, this stimulus elicits minimal excitation. When the signal deviates from the standard, the reaction of the command neuron is greater. The command neuron selectively depresses the signal that was used in instruction. The dotted line (horizontal) indicates the level of excitation of a command neuron prior to instruction.

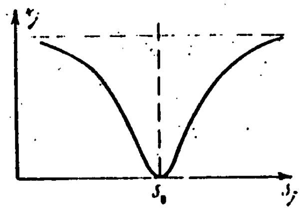

Figure 26.
Command neuron as a readjusting filter blocking a constant signal

Instruction as connection of detectors to a command neuron. When detectors are disconnected, the coefficients of their communication with the command neuron diminish as these communications are used. As a result, the command neuron, which selectively blocks the instructing signal, becomes a cut-off filter precluding appearance of a reaction to this stimulus. Connection of detectors to a command neuron consists of increasing the coefficients of communication between detectors submitted to the stimulus and the command neuron. The excitation vector, which appears under the influence of the stimulus on the population of detectors, performs the function of controlling the communication coefficients between detectors and command neurons. As a result of delivery of the stimulus many times, the communication vector that connects the detectors to the command neurons is transformed and becomes collinear with the excitation vector (Figure 27). Now the stimulus generates an excitation vector on the set of detectors that is collinear with the communication vector, and it elicits a maximal reaction by the command neuron. All other stimuli, which generate excitation vectors that are not collinear with the vector of communication with the command neuron, elicit milder reactions (Figure 28). Thus, in the course of change in communications, the command neuron becomes a selective filter that reacts only to a specific stimulus.

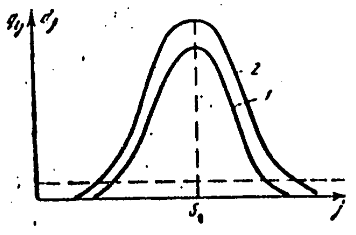

Figure 27. Connecting detectors to command neuron

j) detector No
q_{lj}) communication coefficient
d_j) level of detector excitation
1) detector excitation curve created by stimulus
2) profile of transformed communication coefficients

vertical dotted line--position of instructive stimulus
horizontal dotted line--initial level of coefficients of communication between detectors and the command neuron

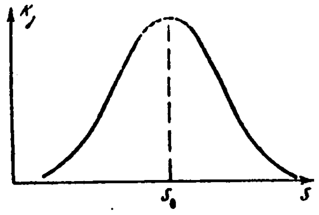

Figure 28.
Command neuron as a readjusting filter which amplifies the signals

In Figure 28, changing stimulus S, which generates a variable excitation vector D on secondary detectors, is plotted on the x-axis and the reaction of command neuron k_j to the variable stimulus. The maximum reaction occurs to the S_0 signal that was used for instruction and created a modification of communication vector Q* (vertical dotted line).

Instruction as change in communication between detectors and the command neuron as a result of effect of reinforcement input. The above cases of disconnecting detectors from the command neuron or connecting them were determined exclusively by the signals that passed through these communications. Disconnection--connection, which depends on other inputs on the same command neuron is another form of instruction. Let us consider the command neuron with two types of inputs: stable and flexible, which alter the magnitude and sign of the reaction. A change in efficiency of the flexible input is determined by which of the stable inputs functions simultaneously with the flexible input or with some lag. The sign of change in the flexible input depends on the sign of the stable input, while the magnitude of change is determined by the number of combinations of flexible and stable inputs. The excitation vector elicited by a specific stimulus alters the coefficients of communication between detectors and the command neuron in accordance with the next delivery of the stimulus through the stable input of the command neuron.

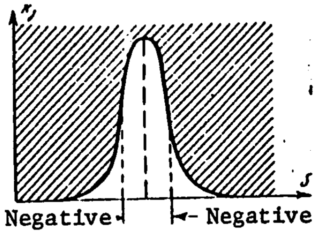

Figure 29.
Change in communications between detectors and command neuron under the influence of positive reinforcement of some stimuli and negative reinforcement of others (vertical dotted line--position of reinforced stimulus S_j)

Let us consider the case where two vectors of detector excitation are given on a command neuron with two stable inputs. These inputs perform the function of reinforcement. When the stimulus is combined with positive reinforcement, the communication coefficients increase and when it is combined with negative reinforcement, they decrease. With a combination of two stimuli with different forms of reinforcement a communication vector develops whose components are determined by the combination number of each flexible input with each of the stable inputs performing the reinforcement function. This complex communication vector now starts to determine the subsequent effects of the stimulus. The excitation vector corresponding to the positively reinforced stimulus and the excitation vector corresponding to the negatively reinforced stimulus, when scalarly multiplied by the formed communication vector, elicits reactions that differ in magnitude (Figure 29). As a result of selective amplification of some communications and depression of others, the command neuron becomes selectively adjusted to the positively reinforced signal. In other words, the effect of the stimulus is now determined by the command neuron input with which it was previously combined. Thus, one can describe formation of a conditioned reflex in the language of change in communications between detectors and command neurons.

Command neurons in the analyzer feedback circuit. It is necessary to discuss command neurons and principles of their communication with detectors when examining artificial sense organs, since the sense organs must themselves be active systems that implement active searches.

The simplest example of active control of sense organs is movement of eyes from one point in space to another in viewing a scene. There are different means of such movement. However, use of a field of command neurons with fixed motor fields makes it possible to provide simple communication between the detectors of target position and command neurons that move the eyes to view the target. The flexibility of command neurons makes it possible to shift the glance on this basis in response to previously ineffective signals, for example, human verbal commands. Introduction of command neurons of a higher hierarchic level makes it possible to move over complex trajectors, assembling them from elements represented by different command neurons of a lower level.

Conceptual reflex arc. The combination of receptors, detectors of command neurons and effector units forms the conceptual reflex arc. The mechanism of coding a signal by channel number by means of detectors forming a multilayer analyzer is used as the main principle of its organization. The most important characteristic of higher level detectors is their invariance, which is achieved as a result of controlling the communications of one set of detectors by the excitation vector generated by another, additional set of detectors. The system of invariant detectors makes it possible to represent exogenous signals on the endogenous screen of the robot, regardless of its own movements in relation to the external environment. The actuating functions of the robot are implemented by command neurons on which converge specific sets of detectors. The priorities of command neurons are changed by means of modulating neurons that are specific to a given situation, which create control vectors for redistribution of comman neuron priorities.

The instruction process is considered as disconnection--connection of detectors to the command neuron. A distinction is made between two types of instruction: dependent only on the stimulus and dependent on the combination of stimulus and reinforcement.

Stimulus-dependent instruction is determined by the number of repetitions of the signal that alters the coefficients of communication of detectors with the command neuron. Reinforcement-dependent instruction is determined by detectors converging on the command neuron that function simultaneously with the stable input of this command neuron.

Passage of signals in conceptual reflex arc: the external signal creates, through receptors, an excitation vector in primary detectors, and it determines the excitation profile of output detectors. This set of excitations is rerouted to invarianted detectors. The response [operation] of the command neuron depends on the priority of the reaction, distinctions of the signal and instruction procedure (Figure 30). This can be described as follows. Signal S, which acts on receptors, induces an excitation vector in them. An excitation vector appears in primary detectors. This leads to selective excitation of the set of secondary detectors. The reactions of command neurons are determined by the contribution of excited detectors, modulating neurons and change in communications between command neurons and detectors during instruction. Lateral inhibition, which is shown by the arrows between detectors, sharpens their selectivity. It also provides for uniqueness [solitary] of excitation of command neurons. The reaction at the output of the entire system is determined by the excitation vector in the set of mononeurons. In the generalized form, the operation of translation of signals in the conceptual reflex arc can be described as matrix multiplication. Let P be the matrix of receptor excitation, A the matrix of communication of receptors with primary detectors, F the matrix of excitation of primary detectors, C the matrix of communication of primary detectors with secondary detectors, D the matrix of excitation of secondary detectors, Q the matrix of communication of secondary detectors with command neurons, K the matrix of excitation of command neurons and $K_{j\max} \Rightarrow R_j$ the transition from the maximally excited command neuron to the reaction that is linked with it. Here, PA = F, FC = D, DQ = K.

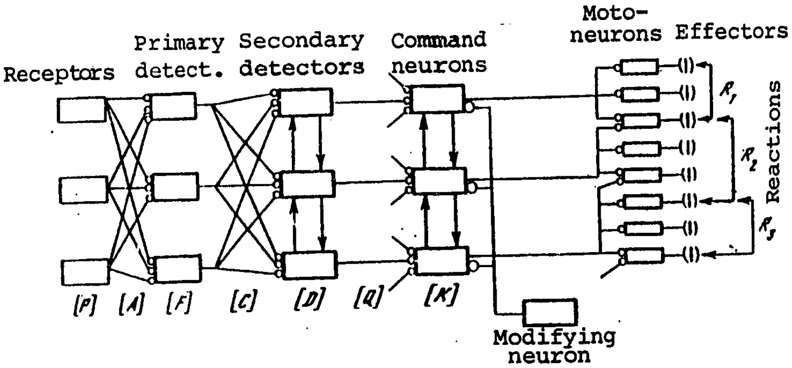

Figure 30. Conceptual reflex arc

[P]--matrix of receptor reactions elicited by stimulus
[A]--matrix of communication between receptors and primary detectors
[F]--matrix of excitation of primary detectors
[C]--matrix of communication of primary detectors with secondary ones
[D]--matrix of excitation of secondary detectors
[Q]--matrix of communications of secondary detectors with command neuron
[K]--matrix of excitation of command neurons

The discussed principles make it possible to create systems of neuron-like elements, the internal conceptions [representations] of which coincide in many respects with the internal conceptions of man, while the reactions reproduce conditioned reflex reactions.

Hereafter, attention is given mainly to artificial sense organs. Command neurons and changes in communication of detectors with command neurons are mentioned only to the extent that they are necessary for the control of sense organs.

CHAPTER 3. INTENSITY ANALYZER

Model of analyzer of intensity. According to the general principle of coding by channel number, coding of light intensity is done by a multilayer system (Figure 31). There are receptors in the first layer of such an analyzer. There are two types of receptors: rods and cones. Three types of cones have different curves of spectral sensitivity to different wavelengths of monochromatic radiation. The reactions of all receptors as a function of light intensity are described by a hyperbolic tangent (in the mean range of sensitivity, this function can be replaced with a logarithmic one (Lipetz [18]).

The signal from the receptors travels to the input of primary detectors of two types. The threshold and coefficient of communication beween receptors and primary detectors are regulated by horizontal cells [19, 20-21].

The characteristics of primary detectors are described according to the general principle by a cosine or sine, the argument of which is a certain function of stimulus intensity (Appendix 2). The characteristics of sensitivity of primary detectors are defined in the range of argument values of 0 to 180°. It is assumed that a primary detector, which is an analogue of a B neuron, has sinusoidal characteristics and the analogue of a D neuron has cosinusoidal characteristics [23, 24].

After the layer of primary detectors with gradual characteristics there is a layer of secondary detectors selectively adjusted to a specific stimulus intensity.

In Figure 32, light intensity I (logarithmic scale log I) is plotted on the x-axis and level of excitation of individual secondary detectors d_i with different levels of input signal intensity is plotted on the y-axis. Different detectors are excited to a maximum with different levels of stimulus intensity. With a change in signal, the excitation maximum shifts from one detector to another.

The controllable threshold of communication between receptors and primary detectors makes it possible to broaden the dynamic range of the entire system, retaining high sensitivity to change in illumination. With increase in intensity of light, the characteristics of primary detectors shift in the direction of higher intensity and with decrease, they shift toward lower ones. One can select a response shift in such a way that the change in light intensity would elicit maximum change in activity of primary detectors.

Operation of the model can be described as follows. With illumination, the signal from receptors excites primary detectors to a certain level. The level of excitation of primary detectors is determined by components of a two-dimensional excitation vector (Figure 31).

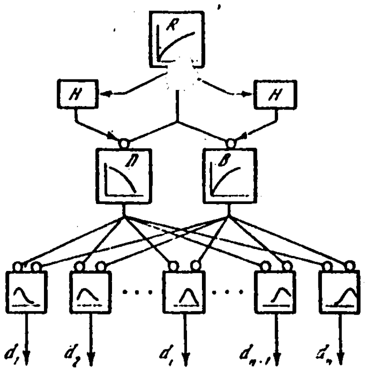

Figure 31.
Structure of local intensity analyzer

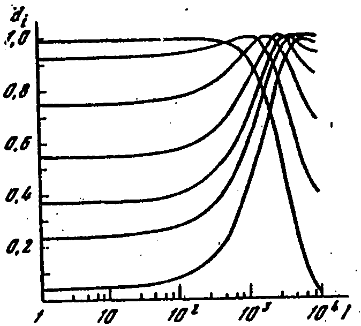

Figure 32.
Selective responses of secondary detectors of intensity

In turn, the signal from B and D neurons goes to the input of secondary detectors and excites them. We find that one of these detectors is more excited than any other input detector. The number of the primary detector with maximum excitation unequivocally determines subjective perception of stimulus brightness. The number of the secondary detector with maximum excitation is unequivocally related to the direction of the two-dimensional excitation vector. With change in stimulus intensity, the direction of the excitation vector changes in the range of the first quadrant, i.e., from 0 to 90°. If we assume that one of the primary detectors is subject to maximum excitation in the dark (D neuron) and another has a zero signal at the output (B neuron), a vector with zero direction corresponds to this case. A vector with zero direction corresponds to the weakest stimulus. With increase in light intensity, the direction of the excitation vector changes, coming close to 90°. A value of stimulus intensity, with which the subjective sensation does not change in the course of adaptation, corresponds to a 45° angle position of the excitation vector. In Figure 33, all of the diversity of secondary detectors of the local intensity analyzer is situated on the circumference within the angle of the first quadrant, which corresponds to different combinations of excitation of two primary detectors. Excitation of a type D primary detector is plotted on the x-axis and excitation of a type B primary detector is plotted on the y-axis. The position of the excitation vector changes as a function of force of stimulus, which corresponds to shifting of excitation maximum from one secondary detector to another, reflecting strong (1), average (2) and weak (3) signals.

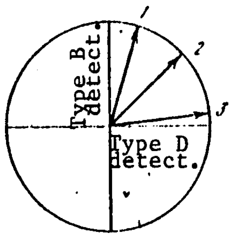

Figure 33.
Space of perception of intensity

However, we know that in the absence of light man does not perceive the color black. Under these conditions, his perception is characterized as "something gray." The typical distinction of the human and animal light intensity analyzer is that the brightness of the signal is measured in relation to a certain average level, which corresponds to absence of signal at the input. Changes in brightness occur in both directions, increase and decrease in relation to the level of the "retina's own light."

Simultaneous contrast. In the case of overall illumination of the retina, perception of black as less bright than the "retina's own light" is impossible. Perception of "black" occurs when there are sections of the retina with considerably lower than average illumination. Thus, perception of "black" occurs only when two adjacent sections of the retina are illuminated to different degrees. This means that the blackening effect is the result of interaction of at least two local analyzers of intensity.

According to the general principles of organization of sensory systems, there is interaction between local analyzers that enhances differential sensitivity of the system as a whole. This interaction occurs with the participation of inhibitory communications between analogous primary detectors of different local analyzers. Formally, this interaction is described by transformation of the corresponding excitation vectors. The resultant vector in a given analyzer equals the initial excitation vector in the same analyzer minus the excitation vector generated in an adjacent local analyzer multiplied by the coefficient of interaction. The direction of the resultant vector does not necessarily coincide with the direction of the initial excitation vector. If the direction of the excitation vector changes, there is also a change in the number of the detector with maximum excitation.

Let us assume that there is no signal at the input of one analyzer and that the input of another is illuminated. Absence of signal corresponds to an excitation vector with zero direction. However, as a result of interaction, the excitation vector goes beyond the first quadrant, since the reaction of the B primary detector becomes negative. This is associated with decline in level of excitation of the D neuron.

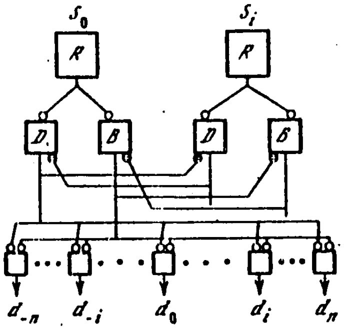

Figure 34.
Concurrent contrast during interaction of two intensity analyzers
R) receptors
B, D) primary detectors
d_i, $i=1, \ldots, n$) secondary detectors of one local intensity analyzer
d_{-i}, d_i) secondary detectors of black and white stimuli, respectively
d_0) gray color detector

The characteristics of primary detectors change under the influence of concurrent contrast: a negative part appears in B detectors with illumination of adjacent regions, whereas the excitation level drops in the D detector. Interaction of stimuli in two local intensity analyzers is illustrated in Figure 34. Two stimuli, S_0 and S_i, act on two local intensity analyzers. Analogous primary detectors are linked by lateral inhibition (D neuron with D neuron, B neuron with B neuron). Appearance of black shades is related to the fact that the excitation vector shifts to the fourth quadrant, where primary type B detector is inhibited (striped circles represent inhibitor relations and white show positive relations).

Thus, different sections of primary detector responses can occur on several different neurons. In this case, B and D neurons of adjacent local analyzers are involved in formation of primary detector responses. The positive segment of the response is formed by the primary detectors of a given local analyzer and its negative segment by primary detectors of adjacent analyzers.

This model is characterized by the fact that signals from both its own primary detectors and from primary detectors of adjacent analyzers go to the secondary detectors of the local intensity analyzer. The set of secondary detectors can be divided into two subsets: all detectors that code the direction of the excitation vector in the first quadrant are referable to one subset. They operate when there is overall illumination of the retina. The other subset consists of detectors that code the directions of the excitation vector that go beyond the first quadrant. There will be detectors in the second subset that code the sensation of black, i.e., sensations that arise when illumination of the retinal segment is lower than the average level, from which brightness gradations are measured (Figure 35). As long as only a signal from its receptive field travels to the input of primary detectors of the local analyzer and there is no inducing signal from adjacent analyzers, only some of the intensity detectors function, which correspond to increase in intensity in relation to the retina's light. If there is an inductive signal from an adjacent section, detectors that measure gradations from gray to black function.

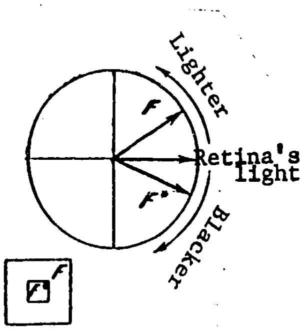

Figure 35.
Appearance of shades of black as a turn of the vector into the fourth quadrant under the influence of an inductive field
F*) excitation vector of test field
F) inductive field vector

To construct secondary detectors, determination is first made of the van of excitation vectors for which output detectors must be constructed. Then a communication vector is assigned to each detector that is collinear to the corresponding excitation vector. It is assumed that the modulus of all communication vectors is constant.

Properties of different elements of the model of intensity analyzer. In the absence of illumination of the retina, the excitation vector has a zero direction. The secondary detector, which codes neutral gray (intrinsic gray) has maximum excitation. With increase in illumination, the B detector becomes increasingly excited, whereas excitation of the D detector diminishes. An increase in illumination corresponds to increase in angle of rotation of the excitation vector to 90°, which is associated with a shift of excitation maximum from the detector of "intrinsic gray" in the direction of detectors of more brightness. The level of intensity required to shift the excitation maximum from the detector of "intrinsic gray" to an adjacent one determines the absolute threshold of intensity perception.

With change in illumination there is a change in level of excitation of primary detectors. The reaction of different output detectors of the model as a function of illumination can be calculated on the assumption that the respones of primary detectors are cosine curves, the argument of which is the overall receptor signal delivered to their inputs. The data obtained are similar to the characteristics of intensity detectors found for the rabbit's visual cortex [25].

Neurons involved in coding intensity can be classified as so-called brightness cells [25]. Spectral sensitivity of brightness cells is characterized by the visibility [luminous efficiency?] curve. The visibility curve is determined experimentally, establishing the intensity of monochromatic light at a given wavelength so that its brightness would be constant.

The spectral characteristics of different neurons are determined by finding the intensity of monochromatic light at a given wavelength, at which neuronal activity reaches a certain fixed level. Evidently, the spectral characteristics of primary detectors are determined by the spectral characteristics of receptors at the model's input. Either rods (with low illumination) or cones (with high illumination) can serve as receptors in the model. Thus, with low intensities, the spectral characteristics of primary detectors are determined by the spectral properties of rhodopsin and coincide with the scotopic curve. With high illumination, they are determined by the overall spectral characteristics of all three cones and correspond to the photopic visibility curve.

Apparently, the reaction of any detector neurons of the model will not change if there is no change in magnitude of the overall receptor signal delivered to the input of primary detectors. The reaction of secondary detectors does not change either.

Thus, the spectral properties of all neurons of the model of light intensity analyzer have the same appearance; it is described by a photopic visibility curve with high intensities, i.e., all of the neurons in the intensity analyzer model are, in the classification of deValois [26], brightness cells.

Subjective differences with changes in light intensity. According to the spherical model of signal discrimination, the subjective space of perception of stimulus intensity is described by the circumference of a single radius. The subjective distance between stimuli is determined by the angle formed by the corresponding excitation vectors or length of the arc on which this angle is based. It would be logical to select the zero direction vector, which corresponds to "intrinsic gray" as the reference point. In this case, subjective brightness of the stimulus equals the angle formed by the zero vector and given excitation vector.

The model satisfies the function that is known in psychophysics as the law of Weber-Fechner [27].

In the model, the threshold increment of intensity is determined as a value, at which the excitation maximum shifts from one secondary detector to the next one. If the density of detectors on the circumference is constant, the threshold increment of intensity is determined by a value at which the excitation vector turns by a certain fixed angle; the turn angle is unrelated to the current value of stimulus intensity.

In other words, if we operate with distances in the subjective space of the model, the differential threshold measured in angular units is a constant. If we know this value, we can determine the threshold increment of intensity that elicits a change in sensation for the first time.

After determining the threshold increment of intensity, we can calculate the Weber fraction for the model (Figure 36).

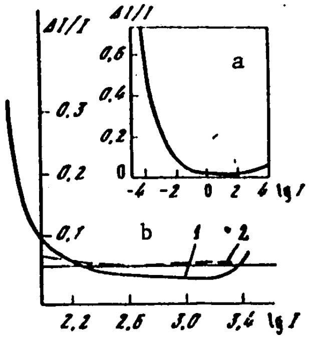

Figure 36.
Curve of Weber's fraction for man and model

lg I) logarithm of stimulus intensity
ΔI/I) relative differential threshold, where ΔI is threshold change in stimulus intensity
a, b) curve of Weber's fraction for man and model, respectively
1) curve of Weber's fraction in the case where receptor sensitivity is described by a hyperbolic tangent
2) by a logarithmic function

If the sensitivity of receptors to stimulus intensity is described by a logarithmic function, the Weber fraction is constant. If the characteristics of the receptor are represented by a hyperbolic tangent, the Weber fraction is constant only for middle intensities: with lower or higher intensities it increases for the model. The Weber fraction as determined in psychophysical experiments behaves similarly. However, in the model, the range of intensities for which the Weber fraction is constant is narrower than the one for man. This is attributable to the fact that the calculations did not take into consideration the effect of a shift of detector responses along the intensity axis. The increase in Weber's fraction with strong intensities is related to the fact that saturation of primary detectors occurs. In order to alter the reaction of primary detectors by a magnitude at which the excitation vector would turn by the threshold angle there must be a large increment of intensity (Appendix 2).

Steven's law. The subjective distance between stimuli is determined by the angle between the corresponding excitation vectors. If one of the vectors is fixed and corresponds to "intrinsic gray," while the other is arbitrary and corresponds to a stimulus of arbitrary intensity, the angle between vectors as a function of intensity of the arbitrary stimulus is an analogue of Steven's psychophysical law (Figure 37) [28]. The angle of excitation vector rotation as a function of the logarithm of stimulus intensity was calculated and found to be close to the experimental data of Stevens. For weak and middle intensities this function is a straight line. With strong intensities it is curved: in order to elicit the same increase in brightness as with weak intensities, one must increase stimulus intensity more and more.

However, there is also some difference between experimental and estimated characteristics: the experimental response deflects down with mild intensities of light, whereas the estimated function does not deviate from the straight line. The nonlinearity of this function increases for man if the assessment of stimulus brightness is made after preliminary adaptation to a certain stimulus. The greater the intensity of the adaptive stimulus, the greater this deviation [28, 29].

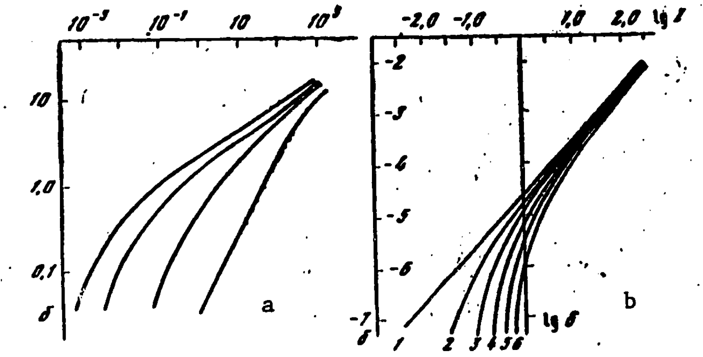

Figure 37. Stevens' function for man and the model

lg I) logarithm of stimulus intensity
δ) logarithm of rank evaluation of intensity or logarithm of subjective distance calculated in the model (curves 2-6 calculated with consideration of shift in characteristics of primary detectors in relation to the intensity scale with the adaptive effect of high-intensity stimuli)
a) function found experimentally for man
b) function calculated for the model

This effect can also be reproduced in the model if we consider the mechanism of raising the threshold when the signal is transmitted via the receptor--primary detector channel. With increase in illumination intensity there is intensification of the signal at the receptor output, which leads to intensification of the signal at the output of horizontal cells. In turn, amplification of the signal at the output of horizontal cells leads to elevation of the threshold of the receptor--primary detector channel. As a result of these processes, only signals that exceed this threshold reach the input of primary detectors. This provides for a shift of primary detector responses in the direction of high intensities, which prevents saturation thereof. As a result, the model does not perceive intensities that are elicited in receptors by a signal that is smaller than the threshold of the receptor--primary detector channel. Deflection from a straight line with reproduction of Steven's law in the model is a consequence of this. The higher the illumination of the adaptive stimulus, the higher the threshold and the greater the initial range of intensities to which the model remains insensitive.

Adaptation of primary detectors of intensity. Under the influence of light on the main receptive field of a local analyzer, the sensitivity of primary detectors diminishes porportionally to the force of excitation. Thus, with high brightness, the sensitivity of a type B primary detector decreases more than that of a type D detector.

This is associated with a turn of the excitation vector in the direction of the vector with a 45° direction, i.e., the perceived brightness of the stimulus diminishes. If, however, the intensity of the adaptive stimulus is such that the output signal of the B neuron is lower than the signal at the output of the D neuron, as a result of adaptation the excitation vector turns from the zero vector toward the vector with a 45° direction. Upon adaptation to dark, the subjective brightness of the stimulus increases. These processes are an expression of the normalization effect in the intensity analyzer.

Since the change in responses of primary detectors persists for some time, even after discontinuing the adaptive stimulus, an aftereffect occurs. The stimulus delivered after prior adaptation generates an excitation vector whose direction differs from that of the vector generated by the same stimulus in the absence of adaptation. Subjective evaluation of brightness changes in such a way that analyzer discrimination increases in the vicinity of the adaptive stimulus. This is manifested by the fact that the subjective distances increase between stimuli in the vicinity of the stimulus intensity at which adaptation occurred.

All of the above considerations can be extrapolated to perception of black, when the main field is surrounded by a lighter inductive field. In this case, it must be borne in mind that the responses of primary detectors are formed by means of both the main and inductive fields.

The aftereffect enables us to explain in part successive images. Indeed, let a bright stimulus be delivered to the main analyzer field. As a result of adaptation to this stimulus, there sill be greater decrease in sensitivity of B detectors than that of D detectors. After this stimulus is discontinued, the background stimulus excites B neurons to a lesser extent than in the absence of the adaptive stimulus. As a result, this background is perceived as being darker than without prior adaptation. This explains the next negative image.

After adaptation to the inductive field in the absence of a stimulus to the main field, the sensitivity of the B neuron becomes greater than that of the D neuron. This leads to appearance of a positive next image in the segment of the main field.

The following factors must be taken into consideration to explain completely the dynamics of successive images: occurrence of oscillations in the set of detectors as a consequence of inertia of inhibitory and excitatory connections between them; change in threshold under the influence of the adaptive stimulus in the receptor--primary detector channel.

Adaptation is combined with concurrent contrast, which is the consequence of inhibitory relations between analogous primary detectors referable to different local analyzers. Thus, D neurons of one segment of the retina have an inhibitory effect on D neurons of another segment. There is analogous mutual inhibition between B detectors.

Let us consider two cases. In the first case, let the stimulus affect only the main field of the local analyzer. The delivered stimulus increases activity of the B neuron and decreases activity of the D neuron. Conversely, in adjacent segments, B neurons are not excited while D neurons show maximum excitation. As a result of lateral inhibition between primary detectors of different local analyzers, D neurons of the main field are strongly inhibited by D neurons of the inductive field, while B neurons of the inductive field are strongly inhibited by B neurons of the main field. Then the components of the excitation vector on the main field will change so as to correspond to stronger stimulation. In turn, changes in components of the excitation vector in adjacent local analyzers whose receptive fields are not illuminated correspond to a "weaker" stimulus. This is perceived as the color black.

In the second case, let the main and inductive fields be equally illuminated. The degree of excitation of primary detectors of both local analyzers is the same. As a result of interaction of analogous primary detectors of two local analyzers, the degree of excitation will diminish in all primary detectors, but the proportion will remain unchanged and, consequently, there will not be a change in direction of the excitation vector either. This means that there is also no change in the number of the secondary detector with maximum excitation. Thus, if the main and inductive fields are equally illuminated, subjective brightness of the stimulus does not change.

This effect differs from lateral inhibition usually discussed in the literature [30-32] in that it occurs between homonymous detectors.

If the main and inductive fields are equally illuminated, as a result of ordinary lateral inhibition the signal at the receptor output will diminish everywhere by the same magnitude. There will also be a change in the signal going from receptors to primary detectors. As a result, there will be a decrease in excitation of B detectors and increase in that of D detectors. This corresponds to a decrease in stimulus brightness. Thus, uniform illumination of the entire retina in the presence of lateral inhibition on the receptor level leads to a decrease in perceived brightness of the stimulus. However, in the case of inhibition between homonymous primary detectors, there is no change in perceived stimulus brightness.

CHAPTER 4. COLOR ANALYZER

Construction of model of color analyzer. In accordance with the general pricniples of constructing sensory analyzers, the model of a color analyzer is comprised of a layer of receptors, layer of primary detectors and layer of output, secondary detectors (Figure 38).

There are three types of cones in the receptor layer--R, G and B--each of which has selective sensitivity to monochromatic radiation with different wavelengths: R is the cone that contains erythrolabe as pigment, which is the most sensitive to long-wave radiation, and maximum sensitivity is obtained at a wavelength of $\lambda = 570$ nm; G is the cone containing the pigment chlorolabe, which is the most sensitive to the middle-wave segment of the visible spectrum, with maximum sensitivity at $\lambda = 535$ nm; B is the cone containing cyanolabe, which is the most sensitive to short-wave radiation, with maximum sensitivity at $\lambda = 445$ nm [33]. As shown by Dartnall [34], the characteristics of cone sensitivity as a function of frequency of monochromatic radiation have the same appearance with accuracy of up to a constant factor [multiplier]. It is assumed that thereafter the characteristics of cones are described by the function of Dartnall. On the whole, these three cones cover the range of visible light waves from 380 to 750 nm.

Signals from cones with different weights and different signs go to the input of primary detectors forming three opponent pairs of cells: 1) pair of neurons excited by red and inhibited by green (red--"+"; green--"-") or, on the contrary, inhibited by red and excited by green ("-"--red, "+"--green); 2) pair of neurons with "+"--blue, "-"--yellow, or "-" blue and "+" yellow); 3) pair of neurons with "+"--black and "-" white, or "+" white and "-" black. Each pair of opponent cells corresponds to one primary detector. The presence of a pair of cells (rather than one) is necessary to separate the excitation and inhibition channels converging on the input of secondary detectors. Thus, the set of three primary detectors (three pairs of cells) describes the components of a three-dimensional excitation vector, and each pair of opponent cells forms only one of its components (Appendix 3).

We should explain why the three types of cones cannot directly determine the components of the three-dimensional color vector of excitation. When the cones are exposed to light of any spectral composition, their reaction presents the same sign, which is determined by the hyperpolarizing effect of light on them. Consequently, if the response of the cones would directly determine the components of the excitation vector, the latter could not go beyond the range of one octant, and then the subjective distances between colors would be small. To increase the distance between colors one must use the entire three-dimensional space. The components of the excitation vector should change in sign with change in spectral composition of the stimulus. This is achieved by the fact that the cone signals travel to primary detectors with different signs and weights.

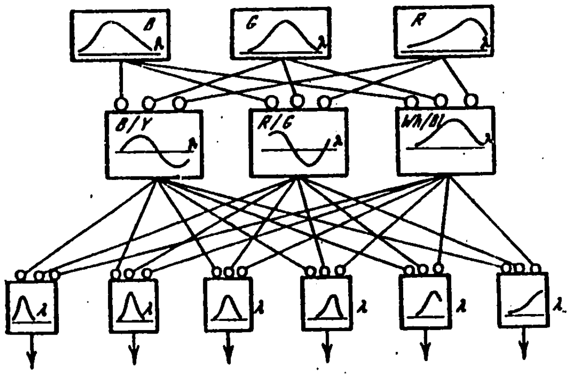

Figure 38. Structure of color analyzer

The first element of signal transformation after the receptors are horizontal cells connected to the cones. The three types of horizontal cells correspond to B/Y, R/G and Wh/Bl elements of the model on the level of bipolar cells. Mutually opposite pairs are formed. Neurons have been found on the level of the visual cortex that are selective for a specific color tone.

In accordance with the spherical model, the characteristics of opponent cells must satisfy the sphere equation. Indeed, a study of the responses of horizontal cells of fish revealed that the sum of the squares of excitation of three types of horizontal cells by equally bright stimuli equals a constant, thus satisfying the sphere equation.

In Figure 39a, the coordinates of color space are given by the excitation of three types of opponent neurons, B/Y, R/G and Wh/Bl representing primary detectors. The sum of the squares of excitation of these detectors for equally bright stimuli is a constant. The modulus $|\Lambda(\lambda)|$ = const. is the radius of the sphere where secondary detectors are localized. The vertical angle of the excitation vector determines saturation and the horizontal angle, the color tone. Detectors selectively adjusted to specific wavelengths of monochromatic radiation form a curve on the sphere that is connected to detectors adjusted to a mixture of red and violet, which corresponds to purples. (B/Y) is the reaction of the opponent primary "blue--yellow" detector, (R/G) is "red--green" and (Wh/Bl) is "white--black." The solid line on the sphere shows the line of monochromatic colors.

In Figure 38b, the color circle is obtained as a projection of the color sphere on plane R/G = x_1 and B/Y = x_2. In the center of the circle is projected the point of the color white, while the projections of monochromatic colors are shown by dots, triangles and squares for different subjects [13]. The wavelength of the indicated color in nanometers is shown near some of the points.

In Figure 39c, the functions of color opponents were obtained by the method of multidimensional scaling on the basis of data on the names of colors [13]. The wavelength is plotted on the x-axis and values of R/G, B/Y and Wh/Bl components on the y-axis.

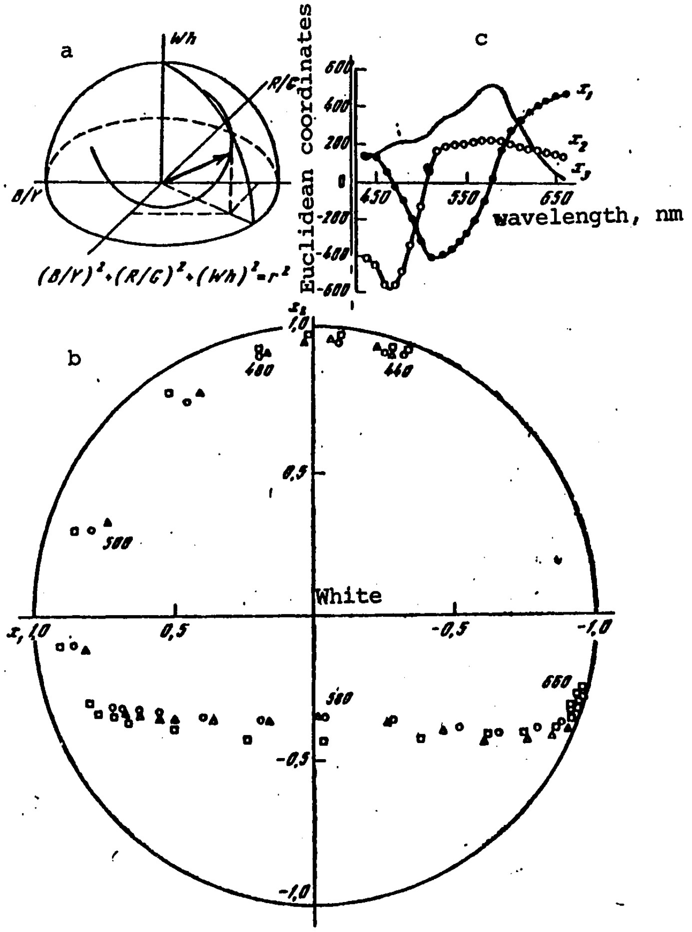

Figure 39. Space of perception of color stimuli

Thus, the entire set of color-selective secondary detectors lies in three-dimensional space on the surface of a sphere [35]. The Euclidean coordinates of this sphere are the levels of excitation of the three types of opponent cells.

The subjective characteristics of color are determined by secondary detectors that "lie" on the surface of the sphere. Here, the horizontal angle corresponds to color tone and the vertical angle to degree of saturation. White is localized at the pole. The line of monochromatic colors lies on the sphere at different distances from the pole. The line of monochromatic colors is connected to the section of purples.

One can construct the system of artificial color vision by the usual scheme. A communication vector is with constant modulus collinear with one of the excitation vectors in three-dimensional color space, formed by the primary detector signal, is ascribed to each of the output detectors.

The function of the color analyzer can be described as follows. When a stimulus of a given spectral composition is delivered to the model's input, hyperpolarization corresponding to the stimulus occurs in the three types of cones. A signal from the cones is delivered to the input of primary detectors (opponent cells [36]) determining the degree of their excitation. A vector of excitation whose direction determines the subjective quality of light that we call color corresponds to a given set of excitations of primary detectors. The signal from primary detectors determines the degree of excitation of each of the secondary detectors, one of which will be excited more than all the others. The number of the secondary detector with maximal excitation determines "perception" of color by the model. The estimated characteristics of secondary detectors as a function of wavelength of monochromatic radiation can be obtained if we know the characteristics of the primary detectors (Figure 40). DeValois [36, 37] discovered color detectors in the lateral geniculate body of a monkey.

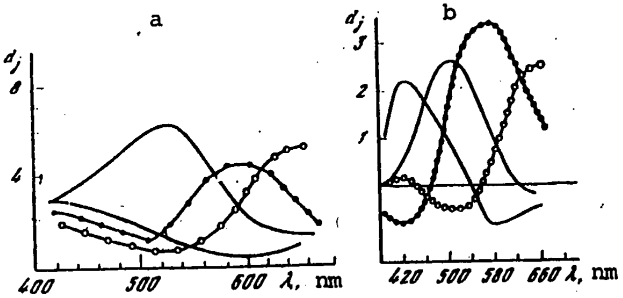

Figure 40. Characteristics of secondary detectors of colors for a monkey and the model

λ) wavelength of monochromatic radiation
d_j) magnitude of reaction of color-selective primate neuron and model element (with change in wavelength, excitation maximum shifts from one detector to another)
a) for monkey neurons
b) for the model

Simultaneous contrast in color analyzer. Like the intensity analyzer, the color analyzer consits of a set of parallel local analyzers. Each of the local analyzers "sees" the outside world by means of a small segment of the retina, from which it receives a signal. We previously named this retinal segment the main field of the local analyzer.

According to the general principle of concurrent contrast, there is inhibitory interaction between homonymous primary detectors of different local analyzers (Figure 41). Two stimuli, the main one, S_0 and inductive one S_i, act on two local color analyzers I and II, generating two excitation vectors represented by excitations of corresponding primary detectors of color. Analogous primary detectors are connected by lateral inhibition. If the intensity levels are the same, lateral inhibition alters the color tone and saturation in each segment without appearance of black shades; if the illumination of the inductive field is greater than that of the main field, the excitation vector turns and moves into the other half of the sphere. This is associated with excitation of secondary detectors of color (d_1, d_2, ..., d_n), which are characterized by blackish shades. For this reason the color of the main field acquires a blackish shading. Consequently, primary detectors receive signals not only from receptors of the main field, but those of adjacent fields. Let us call the segments of the retina that are not the main ones for a given local analyzer but influence its function by means of simultaneous contrast relations the inductive fields.

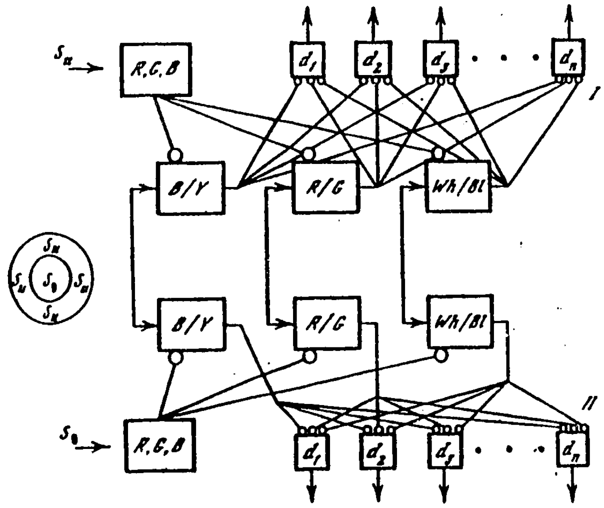

Figure 41. Simultaneous contrast in the color analyzer

In the case of uniform illumination of the entire retina by light of the same spectral composition, a change in spectral composition of light leads to a change in direction of the excitation vector, but it does not exceed the boundaries of the convex cone circumscribed by the line of monochromatic colors.

This statement ensues from the convexity of such a cone. Indeed, light of any spectral composition can be described as the result of the overall effect of its monochromatic radiation components. Since the model is linear, the resultant excitation vector is the sum of vectors generated by the different monochromatic radiations. Since the cone of monochromatic colors is convex, the resultant vector is always within this cone.

Thus, in the case of uniform illumination of the retina, color perception is limited to the monochromatic cone. However, in theory, the range of color perception can be increased. For this, we must know how to obtain excitation vectors beyond the monochromatic cone. Presence of detectors on the sections of the sphere lying beyond the line of monochromatic colors is a condition for effectiveness of such a procedure.

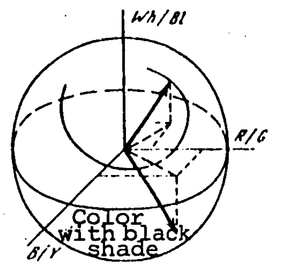

Figure 42.
Appearance of new color shades as a result of influence of inductive field (solid line shows the trajectory of monochromatic colors)

In the case where the main and inductive fields of the color analyzer are illuminated by monochromatic radiations differing in wavelength, the excitation vector determining color perception by the model equals the excitation vector generated by the stimulus in the main field minus the vector corresponding to the stimulus in the inductive field, multiplied by the coefficient of interaction. In the general case, such a resultant vector could go beyond the boundaries of the monochromatic cone, leading to color sensations that would be impossible with uniform illumination of the entire retina (Figure 42). An analogous situation exists in human perception of color. When the main and inductive fields of the analyzer are illuminated by light differing in spectral composition, perception of such colors as brown, grayish brown, brick occurs, which is impossible with uniform illumination of the entire retina.

Thus, as is the case for the intensity analyzer, the set of secondary detectors can be divided into two subsets. One of them includes all the neurons that code colors corresponding to excitation vectors of the monochromatic cone and the other, all the rest of the detectors. These output detectors are subject to maximum excitation only if the stimuli of the main and inductive fields have different spectral composition.

Although the properties of such neurons had not been submitted to experimental study, according to deValois [26], there is inhibitory interaction of the "simultaneous contrast" type in the color analyzer.

The functional significance of inhibitory relations between homonymous primary detectors of different local analyzers is to increase disrcimination sensitivity to two stimuli delivered simultaneously to different segments of the retina. Such interaction leads to increased subjective differentiation of stimuli.

The increase in differential sensitivity to stimuli similar in color to the stimulus on the inductive field inevitable leads to diminished differential sensitivity to other colors. This is due to the fact that, on the whole, the sensitivity of the color analyzer is close to optimal, and it cannot be increased for all colors at the same time: an increase in sensitivity to some colors inevitably leads to a decrease therein to others.

The human color analyzer has analogous properties. It has been shown that illumination of the inductive field with, for example, green color leads to an increase in differential sensitivity on the main field to stimuli that are close to green. However, this is associated with a decrease in sensitivity to other colors, for example, blue [38].

Interaction of the "simultaneous contrast" type provides for some invariance of color perception in relation to the color of background illumination. Indeed, if the main and inductive fields are illuminated by additional background light, the effect of the overall background illumination is compensated by mutual inhibitory signals.

However, in addition to positive effects, interaction of the "simultaneous contrast" type generates a number of negative phenomena. We refer to illusions of simultaneous contrast. Let, for example, the entire screen be illuminated by red light, with the exception of a small light spot. As a result of concurrent contrast, the white spot is perceived by man as being green. We could cite many examples of such illusions.

Moreover, the inhibitory mechanism of "simultaneous contrast" creates the effect of one color being masked by another when delivered successively. The closer the delivered stimuli are in color, the greater the masking effect. The effect of masking of one stimulus by another is attributable to residual lateral inhibition by the preceding stimulus of excitation elicited by the next stimulus. This inhibition is effected via lateral connections between primary detectors, and the closer the stimuli are in color, the greater the inhibition. This is also observed in psychophysical experiments: the closer two successively delivered stimuli are in color, the more they mask one another [39].

Adaptation in the color analyzer. There is an adaptation mechanism in the color analyzer which enhances its ability to discriminate the colors of two successively delivered stimuli. Such enhancement of discrimination sensitivity of the color analyzer is obtained by lowering the sensitivity of primary color detectors proportionally to the level of their excitation by the adaptive stimulus. In the course of prolonged observation of the same adaptive stimulus, there is continuous change in sensitivity of primary detectors and, consequently, there is also continuous change in signal at the detector output which, in the general case, corresponds to continuous change in direction of the excitation vector. In turn, a change in direction of the excitation vector leads to a change in the number of the output detector with maximum excitation and change in perception of stimulus color. Thus, during prolonged observation of a stimulus there is constant change in perception of its color. This phenomenon is called the normalization effect in the color analyzer. According to previously obtained findings, stimuli that excite either only one of the primary detectors or excite all primary detectors equally are not subject to the normalization effect.

Of all the stimuli that are not subject to normalization, only those that excite all primary detectors equally are stable. This means that, in the course of adaptation, all vectors tend toward the vector with equal components. During adaptation, the excitation vectors move toward the vector that has equal components over different trajectories. If an excitation vector has at least two equal components, its trajectory is flat during adaptation and the excitation vector remains in the same plane all of the time. These planes are two-dimensional invariant subspaces of the adaptation operator (Appendix 7).

All the rest of the vectors have a rather complex trajectory: saturated colors shift during adaptation in both the direction of white and the direction of one of the planes that is a two-dimensional invariant subspace of the adaptation operator.

Let there be a plane containing the excitation vector for white. As it intersects the three-dimensional solitary sphere, it forms a certain meridian. By rotating this plane about the vector for white we obtain a family of meridians of the unit sphere of colors. Each color excitation vector can now be described by two parameters: one indicates the meridian on which lies its point of intersection with the unit sphere and the other shows the shortest distance between this point and the point corresponding to white. The former characterizes the chromaticity of the stimulus and the latter its saturation [40, 41].

The normalization effect consists of the fact that, when viewing a stimulus for a long time there is a change, in the general case, in both its chromaticity and saturation. Stimuli corresponding to vectors referable to invariant subspaces of the adaptation vector do not change color in the course of prolonged observation, only their saturation changes.

Monochromatic colors with wavelengths of $\lambda \approx 470$, 492 and 560 nm do not change their chromaticity [14]. In addition to monochromatic colors, there is also no change with adaptation in chromaticity of the color with the following three-stimulus coefficients: $x = 0.495$, $y = 0.155$, $z = 0.35$.

Studies of the model yielded the same data as psychophysical studies.

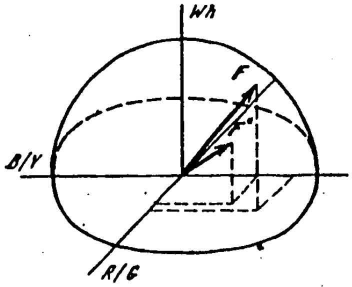

Figure 43.
Shift of end of excitation vector with adaptation to color

We know that chromaticity of a monochromatic light source with wavelengths in the range of $\lambda \approx 470$-487, 507, 565-576 nm does not change during adaptation. In addition to the abovementioned colors, there is also purple, which also does not change its chromaticity during adaptation [42]. Other colors change with adaptation (Figure 43). The original color before adaptation is characterized by different components of excitation vector F. With adaptation, the vector components diminish proportionately to the degree of their excitation. For this reason, excitation vector F* deflects to a position where the components are equal. Saturation of a highly saturated color diminishes, while the color tone shifts to one of the stable colors.

In real neuron nets, changes in sensitivity induced by an adaptive stimulus are restored after discontinuing the stimulus gradually, with some lag. If the stimulus reaches the analyzer input before total restoration of sensitivity of primary detectors, it stimulates primary detectors differently. This means that the same stimulus delivered before and after preadaptation generates excitation vectors differing in direction and elicits perception of different colors.

In analyzing the adaptation effects, it must be borne in mind that they could be elicited by adaptation of detectors in both the main and inductive fields. In the latter case, the effect of adaptation is transmitted via inhibitory connections between homonymous primary detectors of different local analyzers.

These illusions are the price for the gain in discrimination sensitivity that the system acquires because of adaptation. Thus (see Figure 44), after prior adaptation to three monochromatic colors (solid line λ = 500, dash line 555 and dot-dash line 625 nm) there is increase in differential sensitivity of the system, particularly to stimuli whose color is close to the color of the adaptive stimulus. The results obtained with the model coincide with psychophysical data (Figure 44).

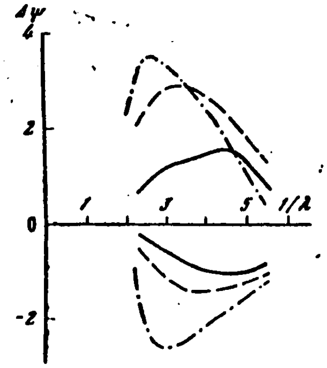

Figure 44.
Increase in differential color sensitivity under the influence of adaptation in the receptor element

1/λ) wave number
Δψ) change in sensitivity (in assessing the influence of receptor adaptation, it must be borne in mind that there is still adaptation of primary detectors)

It was demonstrated experimentally that, as a result of adaptation to red, man becomes more sensitive to a change in saturation of this color. The same applies to adaptation to blue. Concurrently with heightened sensitivity to a change in saturation of the color that is close to the adaptive one, there is a decrease in sensitivity to differences in saturation of colors that are farther away from the adaptive one [43]. Prolonged viewing of a monochromatic stimulus increases man's differential sensitivity to colors that are close to the adaptive one [40].

In the studies of deValois [6], it was demonstrated that there is a decrease in influence of a color on activity of opponent neurons as a result of prolonged adaptation to this color, for example, green. This applies to other colors also.

According to the foregoing, in the course of adaptation the sensitivity of primary detectors to the adaptive stimulus does indeed diminish, and this confirms the initial assumption that the adaptive stimulus influences sensitivity of primary detectors.

Thus, adaptation phenomena in the model correspond to the adaptation effects observed in the human and animal color analyzer, on both the neuronal and psychophysical levels.

In addition to adaptation on the level of primary detectors of color, one must consider adaptation related to a shift in amplitude characteristics of the receptor. Thus, under the influence of white, receptor adaptation equalizes the components of the excitation vector (on the level of primary detector inputs), which prevents development of a chromatic shift. But receptor adaptation disappears faster than adaptation in primary detectors. For this reason, all colors are perceived as being more saturated after adaptation to white. This is attributable to the fact that sensitivity to the "white component" remains low for a long time.

Successive contrast in the color analyzer. After delivery of a color sitmulus, when residual excitation disappears, the sensitivity of primary detectors remains low for some time. The more a given primary detector was excited, the greater this decline of sensitivity. If another color stimulus is now delivered, the excitation vector it elicits will differ from the initial one.

Let us examine three cases of successive color contrast in the model.

1. The adaptive stimulus is a saturated color with a small contribution of a black-white component. In this case, contrast depends primarily on the correlation between blue-yellow and red-green components. If they are equal, the sensitivity of these primary detectors changes equally, and the excitation vector induced by the next stimulus does not change its direction--color is perceived regardless of prior adaptation and there is no successive contrast.

If the blue-yellow or red-green component dominates, its sensitivity diminishes more in the course of adaptation. As a result, the excitation vector turns in the direction of the closest stable position. The projection of the excitation vector on the equatorial plane shows that the vector is turning in the horizontal plane. The angle of rotation of the projection of the vector on the equatorial plane corresponds to a change in color tone under the influence of prior adaptation (Figure 45).

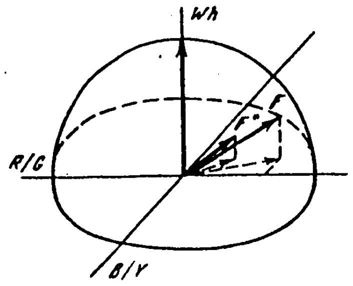

Figure 45.
Successive color contrast with adaptation to saturated color with unequal components of excitation vector

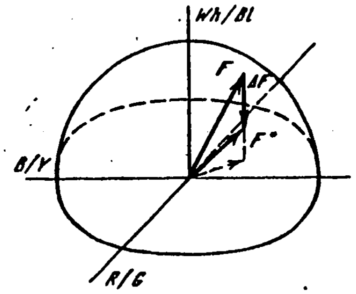

Figure 46.
Successive color contrast in the form of increased saturation after prior adaptation to white

2. Adaptive color--white. In this case there is a decrease in sensitivity of the white-black primary detector, while the sensitivity of the blue-yellow and red-green ones remains high. If we now deliver any color other than white, its saturation increases and will be greater than the saturation of the same stimulus before adaptation. This will happen because, as a result of decrease in white-black component, the excitation vector will turn in the direction of the equatorial plane. This is not associated with change in color tone.

With projection on the equatorial plane, we see that projection of the excitation vector, which retains the direction, increases in magnitude reflecting approximation of the excitation vector to the equatorial plane (Figure 46).

3. Adaptive color--poorly saturated. In this case successive contrast is a combination of two phenomena: increased saturation due to diminished sensitivity of the white component and change in color tone due to greater decrease in sensitivty of the yellow-blue or red-green system (Figure 47).

Thus, all cases of successive color contrast are directly obtained from a model that includes adaptation of primary detectors.

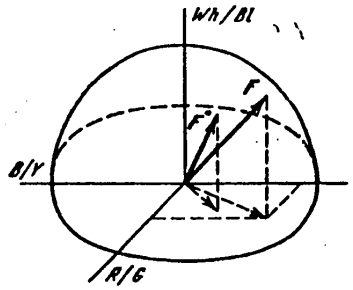

Figure 47.
Successive color contrast in the form of increase in saturation and change in color tone after adaptation to poorly saturated color

- F) position of vector induced by stimulus S before adaptation
- F*) position of vector induced by the same stimulus after adaptation

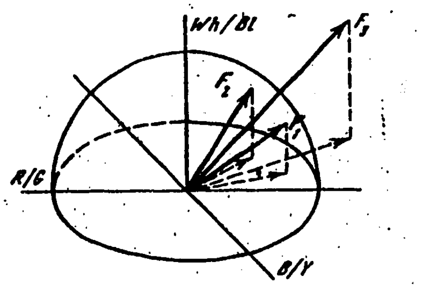

Figure 48.
Summation of two saturated colors of equal brightness

Color mixture. Within the framework of the color analyzer model in question, there is also a simple and graphic explanation of the laws of mixing equally bright colors. If each of two stimuli elicits a specific excitation vector in the color analyzer, the color of mixture thereof is determined by the resultant excitation vector. Indeed, the components of the mixture excitation vector equal the sum of components of the signals making up the mixture.

Let us consider two cases of summation of color stimuli.

1. Mixture of two saturated colors with different color tone. Saturation of color diminishes in relation to a more saturated color because their white components are summated (Figure 48).

When the components of vectors determining color tone are equal but of opposite signs, the color of the mixture becomes white. This is related to the fact that the blue-yellow and red-green components of the excitation vector for such a mixture equal zero. When the components differ in sign and magnitude, the color of the mixture differs from each initial color.

2. White is summated with a saturated color. In this case, the color tone does not change, but saturation of the mixture diminishes. This occurs because of predominant increase in the white component.

Thus, in all cases the saturation of the mixture is lower than at least one of the initial colors. As for color tone, it is either close to the nearest stable position, when the components of the blue-yellow and red-green systems are the same in sign, or deviate from stable positions in the direction of unstable ones, if the components have different signs.

The distinction of this system of color mixture is that it makes it possible to consider the individual effects of color mixing if the individual characteristics of primary detectors are known.

In addition, this system of color mixing, which is based on responses of primary detectors, makes it possible to take into consideration the effect of color adaptation on the result of color mixture.

With regard to color mixture in the model, we have discussed only cases of mixing colors of equal brightness. When colors of different brightness are mixed, the excitation vectors are multiplied by scalars proportional to the logarithm of brightness of mixed color. The resultant color will be determined by the contribution of colors with different brightness to the resultant excitation vector.

One can make a more precise mixture of colors of different brightness by adding the signals in receptors and then finding the values of the components of the resultant excitation vector [44].

This principle of color mixing applies to colors that appear as a result of simultaneous color contrast and that are localized in the opposite hemisphere.

CHAPTER 5. LINE SLANT ANALYZER

Analysis of visual scenes. In describing a scene, one must not only distinguish color and brightness of different elements, but be able to single out different objects. The problem of distinguishing objects often amounts to the problem of distinguishing their outlines--the lines along which an illumination gradient is observed. In order to solve the problem of distinguishing the outlines of objects, it is convenient to consider the visual scene in the form of a scalar field. A value is ascribed to each point of this field that characterizes its illumination. It is not difficult to move from the scalar field to a field of gradients. The gradient of a scalar field is a vector that is determined at each point of the field by the normal to the level of equal illumination. The length of this vector equals the rate of change in illumination in the indicated direction. Knowing the gradient of the scalar illumination field, one can determine the equally illuminated levels that are orthogonal to it at each point of the field.

As a rule, it is very difficult to distinguish the outline of an object, since the image of the scene contains numerous lines, fine details that mask the object. To eliminate this flaw, the following procedure is used: the initial scalar field is submitted to Fourier transformation in order to eliminate fine details from the image. This is associated with suppression of high spatial frequencies. Then, using the inverse Fourier transform, the initial picture is restored, with the exception of fine details. By determining the gradient of the new scalar field the overall outlines of the scene are distinguished.

If it is then necessary to distinguish the fine details of the scene, a Fourier transform is so selected as to suppress the low spatial frequencies without affecting the high ones. Use of the inverse Fourier transform permits restoration of the original picture, but without large details.

Thus, in order to distinguish the overall outline and outlines of fine details separately, the scalar field is transformed twice: in the former case the high spatial frequencies are suppressed and in the latter, the low spatial frequencies. The scalar field, in which high frequencies are suppressed, permits distinguishing elements of the overall outline as we move to the gradient field. The scalar field, in which low frequencies are suppressed, permits distinguishing elements of local outlines as we move to the field of gradients and from it to equally illuminated levels.

In other words, in order to distinguish elements of the overall outline and elements of local outlines, we must determine the gradient of the scalar field twice: with suppression of high spatial frequencies and low spatial frequencies. All of the described procedures are performed with a computer.

After the elements of the outline have been singled out follows the procedure of combining elements into segments. For two elements of an outline to be included in a segment they must be next to one another and the difference in orientation of these segments should not exceed a given threshold level. Segments with common points are combined into structures. Finally, by introducing more complex criteria, the structures are combined into objects. The aggregate of distinguished objects forms the scene. The robot's actions are organized in relation to the distinguished objects.

When using computer techniques, the transition from a scalar field, which represents the initial visual information, to distinguishing segments, structures and objects by transforming the scalar field into a field of gradients and field of equally illuminated levels takes up much time. For this reason, it is of particular interest to discuss the detector approach, which solves the problem of distinguishing outline elements by means of parallel processing of signals on a population of orientation detectors. The final result of such processing is analogous to computer analysis; in both cases the result of converting base data is isolation and definition of orientation of elements of the outline. Subsequent joining thereof into segments, structures and objects of the scene can be done on the basis of usual computer hardware. However, in principle, the introduction of higher level detectors makes it possible to reduce these problems also to coding of segments, structures and objects by channel number.

Neuronal mechanisms of isolating outlines. Visual information is processed in two neuronal systems: neurons that process relatively stationary signals (type X) and neurons that process moving stimuli (types Y and W). Apparently, distinguishing the outline of an object and determining orientation of segments thereof is related to X type neurons, and they are the ones we shall be discussing. These neurons summate the signal from some part of the retina that is called the receptive field. There are two types of receptive fields: with excitatory center and inhibitory periphery (neuron for coding light) and those with inhibitory center and excitatory peripheral (neuron for coding darkness).

In the first case, illumination of the central part of the receptive field leads to excitation, while illumination of the periphery leads to inhibition of the X neuron in question. In the second case, the reverse is observed.

The distinctive feature of X neurons is that they may have different sized receptive fields. In other words, in addition to neurons that summate a signal from a small part of the retina, there are also neurons with large receptive fields. In the former case, the X neurons are sensitive to high spatial frequencies (they distinguish fine details of the image) and in the latter, on the contrary, they are sensitive to low spatial frequencies. As a result of antagonistic relations between the center and periphery of each neuron, the spatial constant component of the signal is suppressed.

On the next level of the external geniculate body, the concentric fields remain, but they become more local as a result of greater inhibition. On the level of the visual cortex, the system of X neurons is localized in the 17th field in the form of columns that unite neurons responsible for an elementary segment of a line with a specific slant in a specific part of the retina. These neurons react selectively only to lines with a specific orientation, performing an operation that is equivalent to change to the gradient of the scalar field of distribution of illumination and finding orientation of elements of the outline. Processing is done concurrently for each retinal segment. Selective adjustment of detectors of line orientation is the result of integration in one neuron of the visual cortex of signals coming from several neurons of the external geniculate body. We must stress another distinction of the neuronal mechanism of detemrining the orientation of outline segments. Neurons that are selective for orientation of elements of image outline consist of neurons with concentric fields of a specific size. For this reason, such a neuron is sensitive not only to a specific orientation of an outline element, but a specific segment of the spectrum of spatial frequencies. A comparison of computer processing of visual information to such processing in real neuronal nets reveals the following. In real neuronal nets, the gradient of the scalar field of illumination is "calculated" for each of the spatial frequencies separately, and in parallel for different spatial frequencies. This yields concurrently both the overall outline and different elements of the image, from large to increasingly smaller ones. Each segment of the retina is represented in the cortex by a neuronal matrix, in which columns correspond to different line orientation and lines correspond to the size of the grain of the image. The sizes of receptive fields of which orientation detectors are constructed increase from the surface into the depth of the visual cortex. In a column with the same orientation of lines, the different orientation detectors represent different spatial frequencies, ranging from high ones on the surface to low ones deep in the cortex. Thus, the retinal segment is represented in the visual cortex by a set of detectors that are sensitive to different orientation and different spatial frequency. If we were to place detectors vertically that are selective to outlines with the same orientation but different spatial frequency, and horizontally the detectors that are selective for different orientations of outline, the local segment of the visual field will be reflected on the field of detectors that are sensitive to orientation and spatial frequency. In other words, what computer techniques do by successive transformation of signals of the primary visual image is done in the neuronal network in parallel, with the use of conception of outline orientation and spatial frequency according to the principle of coding by channel number.

Model of line slant analyzer. Description of the model: According to the main principle of constructing analyzer systems, the model in question must have a layer of receptors, layer of primary detectors and layer of output detectors of line orientation. The receptors, primary detectors and set of output detectors form the local analyzer of line orientation. Such local analyzers represent the entire visual field on the retinal surface, separately for each spatial frequency.

Two systems of detectors must be organized: for white lines on a black background and for black lines on white, using the systems of B and D neurons. However, it is sufficient to construct one of them, and the second is constructed analogously. Let us discuss the construction of such a system. Orientation of the outline is described by one independent parameter, the angle of inclination of the outline in relation to a given coordinate axis. The angle can have any value in the range of 0 to 180°. We must have two independent primary detectors forming components of a two-dimensional excitation vector in order to have the direction of the excitation vector define unequivocally the value of angle ϕ. The characteristics of these primary detectors are a cosine curve and sine curve with a dual angle characterizing inclination of the outline segment in relation to the selected system of coordinates.

One can build primary detectors with optimum characteristics in the following manner. A receptive field is created so that the line centered in relation to it would elicit a reaction, when projected on this receptive field, equaling the sine or cosine of the dual angle, respectively. If all receptors are considered to be identical, the density of their arrangement uniform and the connections with primary detectors the same, the shape of the receptive field is given in polar coordinates as the length of the vector radius that is proportional to the cosine of the dual angle for one detector and the sine of the dual angle for the other detector. The connections of primary detectors with secondary output detectors must be collinear to the excitation vectors of the signals for which these excitation maximums are assumed (Appendix 4).

In this case, the receptive field of the primary detector is in the shape of a figure eight. The question arises as to how to orient the receptive fields of primary detectors in relation to the coordinate axes. In principle, receptive fields could have any orientation. However, one must consider the effect of adaptation of primary detectors. The orientation of receptive fields of primary detectors must be chosen in such a way as to have the adaptation effects in the analyzer of line orientation coincide in the robot and man. Psychophysical experiments have shown that line tilts for which there are no normalization effects and aftereffect correspond to angles of 0, 45, 90, 135 and 180° (Appendix 4). This means that straight lines with such a slant must elicit equal excitation in both primary detectors. In view of the fact that the responses of primary detectors are represented by dual angle cosine curves, lines with a titlt of 0, 45, 90, 135 and 180° will excite equally both primary detectors only when the maximal axis of the receptive field is turned by 22°30' in relation to the x-axis.

Thus, the model has two primary detectors at the input whose reaction equals the cosine and sine of the double angle of inclination of the line measured in relation to the x-axis. The optimum axes of the receptive field of primary detectors are at an angle of 22°30' in relation to the vertical direction coinciding with the direction of the gravity vector.

Since the excitation and inhibition channels must be separated in real neuronal nets, the number of primary detectors must be increased to four. Some detectors effect the positive part of the response and others, the negative.

Output detectors are constructed in accordance with the standard scheme: a communication vector collinear to one of the excitation vectors is assigned to each secondary detectors. This permits calculation of the characteristics of output detectors. One possible variant of such a model is illustrated in Figure 49. In this figure is shown the retinal segment corresponding to the receptive field of the local analyzer of line slant. The four figure eights, two cross-hatched and two not, represent the receptive fields of primary detectors (layer I). Primary detectors have characteristics in the form of the sine and cosine of dual angle ϕ (layer II). The secondary detectors are selectively adjusted to specific line tilts in the range of 0-180°. With a change in line tilt within a local analyzer, excitation maximum shifts from one secondary detector to another. The "+" sign shows the parts of the receptive fields that have an excitatory effect on activity of the given primary detector, while the "-" sign shows the inhibitory region of the detector's receptive field. The quantity of primary detectors was doubled for transmission of negative signals over separate channels. Detectors effecting the negative part of the response receive an exciting signal from areas designated with "-" and inhibitory signals from areas designated "+."

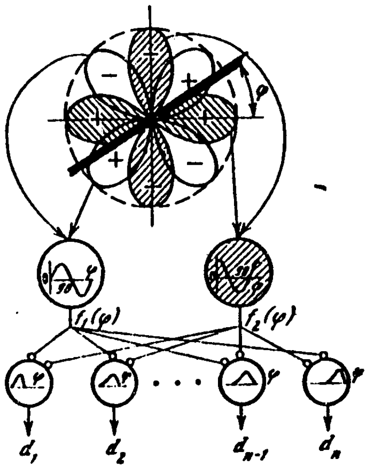

Figure 49.
Structure of local line slant analyzer

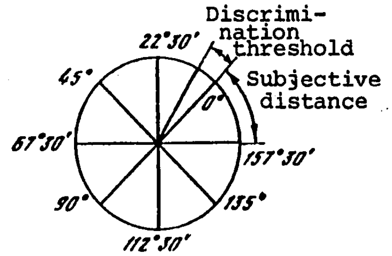

Figure 50.
Space of line tilt perception

Operation of the model can be described as follows. When a given segment of the object outline is delivered to the receptive field primary detectors of the analyzer are excited. The signal from the output of the primary detectors excites secondary detectors, one of which being more excited than all others. The number of the maximally excited output detector unequivocally determines the orientation of the tested part of the outline. Thus, the signal, which generates an excitation vector in primary detectors, creates an excitation profile on the set of output elements. The location of the maximum of this excitation maximum on the set of secondary detectors unequivocally determines the orientation of the analyzed segment of the outline. Two stimuli are indistinguishable if they excite to a maximum the same output detector.

The space of perception of line tilts is illustrated in Figure 50. Excitation of the first primary detector is plotted on the x-axis and excitation of the second primary detector on the y-axis. The excitation vector $F(\phi) = \{\sin 2\phi, \cos 2\phi\}$ intersects the circumference $|F(\phi)| = \text{const}$ at the point where the secondary detector, which codes the signal by the tilt of this excitation vector, is located. The length of the arc between adjacent secondary detectors determines the subjective threshold of discrimination of the line slant.

It must be stressed that there is mutually identical conformity between number of the detector with maximal excitation and direction of the excitation vector. The proposed model transforms signals of physical space represented by slants of a line in the perceptive space of excitation vector directions. The physical space of signals is one-dimensional: it is a certain segment on which the slant of the line could assume any angle, from 0 to 180°. The perceptive space of directions of excitation vectors is also one-dimensional. This is a segment on which the parameter determining the direction of the vector can have any value from 0 to 360°. Thus, the model of the line tilt analyzer causes reflection of one signal as another, doubling its length at the same time. With such reflection, the perceptive distance between two stimuli doubles in relation to the distance in physical space. If the angle between lines equals 30°, the angle between excitation vectors in the perceptive space equals 60°.

Comparison of model to real structure of line slant analyzer: The model of the line slant analyzer consists of two types of detectors that are selective for slant. Both types of detectors have the same characteristics. Consequently, they cannot be classified as primary and secondary according to output responses. However, these types of detectors can be separated according to input: secondary detectors receive a signal only from the four primary detectors, whereas the signal from a set [or numerous] of receptors or ganglionic cells with concentric receptive fields converge on primary detectors. Creutzfeldt et al. [45], concluded on the basis of intracellular recording in a study of detectors of the cat's visual cortex that their selective reaction to slanting of a line is implemented with the participation of only 2-4 cells of the external geniculate body. It is difficult to conceive that such selectivity can be provided by only four nonselective cells with concentric receptive fields. But this can be explained on the assumption that such neurons of the lateral geniculate body are primary detectors. At the present time, the presence of cells that are selective to inclination of a line in the lateral geniculate body has been demonstrated experimentally [44].

The discriminatory property of secondary detectors also ensues from the distinctions of signal coding by the number of the input detector. The perceived value of the coded parameter does not change if the reaction of all output detectors is decreased or increased by the same value. Indeed, this is not associated with a change in the element with maximal excitation.

If, however, part of the response of primary detectors is cut off by inhibition, there will be a change in properties of the model as a whole. This is due to the fact that such an operation alters the direction of the excitation vector. Thus, the responses of primary detectors must be more stable than those of the secondary detectors.

Mixing effect in the analyzer of orientation of slant: If two lines are delivered at different angles in relation to the selected coordinate axis to the same receptive field of a local line slant analyzer, they will have a cumulative effect on primary detectors that is different from the one elicited by each line separately. As a result, one line with an intermediate slant (Appendix 4) is perceived under the joint effect of two lines in the receptive field of one local analyzer. This effect is analogous to the color mixing effect. Burns et al. [46], who studied the mechanisms of Zollner illusions, demonstrated such a mixing effect. The cortical detector reacts by a change in activity to appearance of the second line in its receptive field. It was found that if the distance between two lines is small the cortical neuron reacts to the two lines just as it would to one line with intermediate slant. Thus, there is experimental confirmation of the effect of line mixture in neurons of the cat's visual cortex. An analogous phenomenon occurs in an individual secondary detector of the model. Appearance of two orthogonal lines simultaneously in the receptive field of the local line slant analyzer leads to mutual suppression of primary detector reactions (Appendix 4). This enables us to explain the "torn wire" illusion known in psychophysics [47], which consists of appearance of a seeming break when viewing intersecting telegraph wires at the site of intersection.

Adaptation in the model of line slant analyzer. Normalization phenomenon: If a stimulus that excites primary detectors to a certain level is active at the analyzer input for a long time, according to the general principles the sensitivity of primary detectors starts to diminish, and the higher the level of excitation, the more it diminishes. As a result, the levels of excitation of both detectors strive toward the state where they equal one another. This corresponds to rotation of the excitation vector in the direction of the vector with equal components. In turn, rotation of the excitation vector leads to a shift of excitation maximum from one secondary detector to another and to a change in perception of orientation of the line.

This means that an illusion of change in slant occurs when viewing the line for a long time. This effect is known in psychophysics as the normalization phenomenon. It was first described by Gibson [48, 49] in the late 1930's. If a line is displayed to a man, which deviates slightly from the horizontal or vertical, the illusion that it comes close to the horizontal or vertical arises when it is viewed for a long time. If, however, the adaptive line is strictly horizontal or vertical such an illusion does not occur. In Gibson's opinion, there are two types of lines: stable lines that are not subject to adaptation and lines whose orientation changes and come close to stable when viewed for a long time. Man perceives stable lines as the norm. In the opinion of Gibson, two such norms are represented in the nervous system. A horizontal line activates only its horizontal norm and a vertical line, its own vertical norm. An intermediately tilted line activates both norms. The proportion of stimulation of norms determines the perceived tilt of the line. In the course of adaptation, man strives to alter the norm so that the presented line would become the new norm. Hence the name of "normalization effect."

The question arises as to what happens with a line tilted at 45°. In the course of adaptation it also does not alter its tilt and, consequently, has every right to claim to be another norm. This is not explained in Gibson's theory. In the proposed model of local analyzer of line tilt, there is a simple explanation for the normalization effect. All stimuli that excite either only one primary detector or both to the same degree do not change their orientation during adaptation and, consequently, are not subject to normalization.

Lines with a tilt of $\phi = 0, 45, 90$ and 135°, as well as those with $\phi = 22°30'$, 67°30', 112°30' and 157°30', do not change their slant during prolonged viewing. However, these two groups of lines differ from one another in stability. While the former group is referable to stable lines, the second is unstable. The sensitivity of primary detectors changes under the influence of prior adaptation to a line that corresponds to one of the vectors F, H or G. (Figure 51). The primary detector that was the most excited loses more of its sensitivity. After adaptation to one of the lines, the same line generates excitation vector F* (or H*, or G*) instead of F (or H, or G). A turn of vector F* (or H*, or G*) in relation to F (or H, or G) corresponds to a shift of excitation maximum to another secondary detector and, accordingly, a change in perception of line tilt. The vector components level off as a result of adaptation. The excitation vector shifts to its closest stable position. To restore the fixed position of the line, the stimulus must turn to the same extent as the excitation vector did as a result of adaptation. In this figure, shifting of the excitation vector under the influence of adaptation is illustrated. The direction of the shift depends on the position of the stimulus in relation to a stable position. Stable lines elicit equal excitation of both primary detectors, while unstable ones generate more excitation in one of them.

For this reason, the slightest deviation from unstable tilts leads to drift in the direction of one of the closest stable lines (lines with a tilt of $\phi = 0$, 45, 90 and 135°)(Figure 52). At the same time, when the signal deviates from stable position, the adaptation process acts in the direction that returns the excitation vector to a stable state. Such an arrangement of stable and unstable orientations of the line corresponds to a model with primary detector sensitivity characteristics in the form of functions cos 2 $(\phi + 22°30')$ and sin 2 $(\phi + 22°30')$.

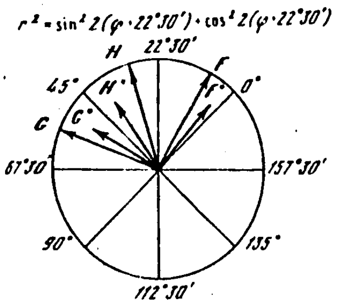

Figure 51.
Change in perception of line tilt after preliminary adaptation to a stimulus, the components of whose excitation vector are not equal
$r^2 = \sin^2 2(\phi+22°30') + \cos^2 2(\phi+22°30')$

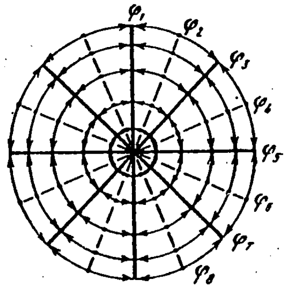

Figure 52.
Line tilts not subject to adaptation (solid line shows stable orientations and dash line shows unstable ones; the arrows show the direction of adaptation drift)

Aftereffect: When the adaptive stimulus is discontinued, there is gradual restoration of sensitivity of primary detectors. For this reason, if a new stimulus is delivered to the input of the local analyzer model before sensitivity of primary detectors is restored, this stimulus will correspond to a different direction of excitation vector from the one when there is no adaptation. The aftereffect is manifested by different perception of the test line delivered after the prolonged use of an adaptive line than without preadaptation.

An analogous effect, also first discovered by Gibson and known as the "aftereffect," is observed when man perceives the tile of a line. If a man is asked to look at a line at a certain slant for a long time and then asked to place the line in a vertical or horizontal direction, the subject will make a mistake. If the angle between the adaptive line and objective vertical is less than 45°, the vertical established by the subject will be rotated clockwise from the true vertical. If this angle is greater than 45°, the vertical set by the subject will be turned counterclockwise in relation to the true vertical. In the former case, the error is considered positive and in the latter, negative [50]. No error is made if the angle between the adaptive line and vertical is zero. According to Gibson, the aftereffect can be explained as follows: there is overestimation of the norm of line tilt during prolonged viewing of an adaptive line. If the adaptive line is close to vertical, the vertical norm shifts clockwise in the direction of the adaptive line (Figure 53a). Concurrently, the horizontal norm shifts in the same direction. If a vertical line is presented to the subject after adaptation, it does not coincide with the vertical norm and is perceived as other than vertical. To restore the subjective perception of vertical, the subject turns the test line clockwise until it coincides with the vertical norm. A positive aftereffect occurs.

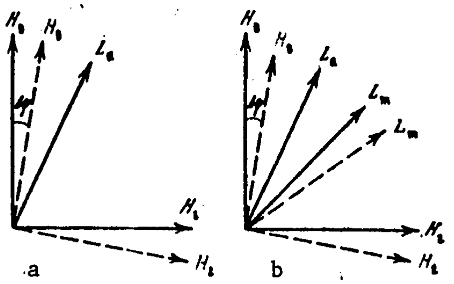

Figure 53.
Normalization effect according to Gibson

H_B and H_2) vertical and horizontal norms
$\Delta\phi$) angle of rotation of vertical and horizontal norm after adaptation to line L_a
L_a) excitation vector corresponding to diagonal test line
L_m) dash-line excitation vector corresponding to diagonal line after adaptation to line L_a

If, however, the adaptive line is closer to the horizontal norm, during prolonged viewing the horizontal norm shifts in the direction of the adaptive line. Concurrently, the vertical norm turns in the same direction. If an objective vertical is presented after this, it will again fail to coincide with the vertical norm and the test line should be turned counterclockwise to restore the sensation of a vertical. A negative aftereffect appears. When the adaptive line is equidistant from the vertical and horizontal norms, there will be no change in the norms and no aftereffect.

If we now take as the test line a line with a 45° tilt, instead of a vertical, and it is equidistant from both norms, the interpretation of Gibson would lead to wrong conclusions. Indeed, if the adaptive line is diagnoal to $45° < \phi < 90°$, both norms turn clockwise as a result of adaptation. For this reason, the true diagonal must be turned clockwise to restore perception of the diagonal, so that it will be perceived as equidistant from both norms. In this case, we should observe the positive aftereffect (Figure 53b).

Kohler et al. [51] made an experimental check of this conclusion of Gibson's, and they found that the experimental data do not confirm the theoretical conclusions of Gibson. Recently, Mitchell et al. [52], who studied the effect of preliminary adaptation on perception of a diagonal line, concluded that, in spite of the theoretical predictions, the aftereffect in perception of a tilted line did not differ in any way from the aftereffects of perception of vertical and horizontal.

The model of a local line tilt analyzer offers a simple explanation for this phenomenon. Let the adaptive line be oriented at an angle $\phi = 22°30'$. With such a tilt, the sinusoid primary detector is excited more than the cosinusoidal one. For this reason, in the course of adaptation the sinusoidal detector's sensitivity diminishes more than that of the cosinusoidal one (Figure 54). If the subject is now shown an objective vertical, it will no longer excite both primary detectors to the same extent. There will be less excitation of the sinusoidal primary detector than the cosinusoidal one. Such excitation of primary detectors corresponds to a line turned counterclockwise in relation to the vertical. To restore the sensation of a vertical, the test line must be turned clockwise by an angle $\Delta\phi$ and then it will again excite both primary detectors equally. Analogous reasoning applies when a diagonal serves as the test line. After adaptation to line $L_{\phi a}$, line $L_{\phi T}$ should be turned counterclockwise by an angle $\Delta\phi$ for it to excite the primary detectors in the same way as before adaptation.

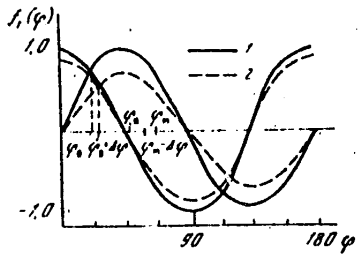

Figure 54.
Normalization effect in the model
ϕ) line tilt
$f_1(\phi)$ and $f_2(\phi)$--reactions of primary detectors f_1 and f_2 to given line with tilt ϕ
1) sensitivity of primary detectors before adaptation
2) after adaptation to line with tilt ϕ_a

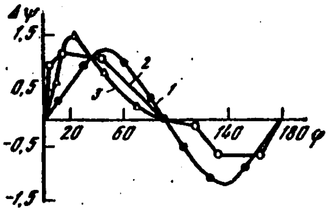

Figure 55.
Aftereffect
ϕ) size of dual angle between adaptive and vertical line (used in experiment as test line)
$\Delta\psi$) systematic error in placing line in vertical position
1) calculated response of model
2, 3) experimental functions determined by Gibson [48] and Campbell et al. [50], respectively

Thus, in the case of an adaptive line with a tilt of ϕ = 22°30', the aftereffect is maximal. If the adaptive line excites both primary detectors equally, the aftereffect equals zero. Thus, with a tilt of ϕ = 45° of the adaptive line no aftereffect is observed. Further increase in tilt of adaptive line leads to a change in sign of aftereffect: the subjective vertical determined by the subject is found to be turned counterclockwise in relation to the objective vertical. The next maximum of negative aftereffect is obtained when the adaptive line is oriented at an angle of ϕ = 67°30'. With an angle of ϕ = 90°, the aftereffect is again absent (Figure 54).

The estimated aftereffect as a function of angle between adaptive and objective vertical lines in the model is qualitatively similar to the analogous experimentally demonstrated response (Figure 55). However, the experimental curve differs from the estimated one. While the aftereffect in the model is symmetrical in relation to point $\phi/2 = 45°$, in man the analogous curve is asymmetrical. Moreover, a maximum effect is obtained with $\phi/2$ = 22°30' for the model and $\phi/2 \approx 10-15°$ in experiments on man. This difference can be significantly reduced if we consider the contribution of lateral inhibition to the aftereffect. In this case, the residual influence of inhibition on the part of the adaptive stimulus appears to push the test stimulus in an opposite direction from the adaptive one. As a result, there is enhancement of the positive effect while the negative one, on the contrary, diminishes.

If a diagonal line is taken as the test line, the aftereffect as a function of angle between adaptive line and this test line has the same appearance as when a vertical is used as the test line. Thus, the aftereffect has the same appearance in the model as the aftereffect when man perceives vertical, horizontal and diagonal lines.

Adaptation on the level of the primary detectors affects differential sensitivity of the entire local analyzer of line orientation as an element of the outline [or circuit]. Differential sensitivity increases to line tilts that are close to the tilt of the adaptive line.

Simultaneous contrast in line tilt analyzer. Inhibitory connections are added between homonymous primary detectors of different local tilt analyzers in order to improve discrimination of line tilt analyzer to two lines presented simultaneously in different points of space. The question of enhancing discrimination of man for two simultaneously exhibited lines had not been submitted to direct experimental investigation. However, there are indirect data indicative of increase in sensitivity. Illusions of widening of acute angles and narrowing of obtuse angles can serve as examples. Let two lines that intersect at a certain angle be shown to a human subject. One line is stationary, L_δ, while the experimenter can alter the tilt of the other line, L_u, which forms the second side of the angle. A third test line, L_T [L_m in figures] is exhibited at some distance from this angle. The subject's task is to place the L_T test line parallel to the stationary side of angle L_δ. It was found that the subject performs this with a systematic error (Figure 56).

If the angle is smaller than 90°, the subject turns the test line counterclockwise in relation to the stationary side of the angle. With angles smaller than 90°, the lines forming the angle seem to draw away from one another, which leads to subjective increase in angle; with angles larger than 90°, the lines appear to be pulled to one another, which leads to subjective decrease in angle they form [53]; if the angle equals 90°, no systematic errror occurs in placing the test line.

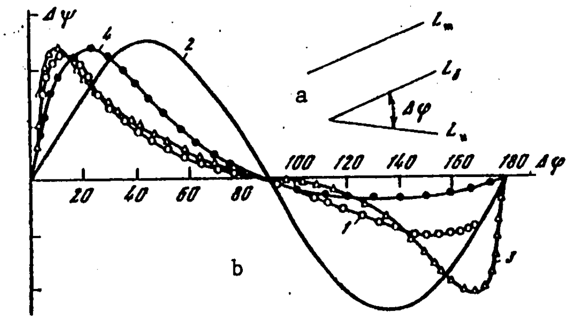

Figure 56. Effect of simultaneous contrast in perception of angles

Δϕ) angle between lines L_δ and L_u
L_δ) line whose tilt was not changed during the experiment
L_m) test line
L_u) inductive line whose tilt was arbitrarily set by experimenter
1) experimentally determined function for man [53]
2, 3, 4) functions estimated for model with following interaction coefficients: $\alpha = 0.2$; $\alpha = 0.02 \exp(-4 \sin \Delta\phi)$; $\alpha = 0.2 \exp(-4 \sin \Delta\phi/2)$ ($\Delta\phi>0$ corresponds to counterclockwise turn of test line L_m in relation to line L_δ)

It can be concluded from the above-described experiment that, as a result of interaction of two lines forming an acute angle, the subjective distance between stimuli increases. If the lines form an obtuse angle, it subjectively decreases. This effect is the consequence of lateral inhibition between analogous primary detectors of different local analyzers of line orientation. Lines that form the angle generate different excitation vectors in different local analyzers of line tilt. The resultant vectors change under the influence of lateral inhibition between analogous primary detectors of spatially different local analyzers. The angle between resultant vectors can be calculated, and one can learn which subjective angle between lines corresponds to it. The angle between resultant excitation vectors will be larger than the angle between initial excitation vectors if the angle between the lines forming it is smaller than 90°. If the angle between lines forming it equals 90°, the angle between vectors will not change.

The closer to one the coefficient of lateral inhibition, the greater the degree of subjective increase or decrease of angle in the model.

With increase in inhibitory interaction, maximum subjective widening of the angle in the model is obtained with increasingly small angles between the lines. The estimated function of subjective change in angle is symmetrical with point $\phi = 90°$. The analogous characteristic obtained experimentally for man is asymmetrical--its positive part is much larger than the negative. One can reduce the discrepancy between experimental and estimated curves by assuming that the inhibitory communications between primary detectors of different local analyzers diminish with distance between their receptive fields. If we accept that such a decrease in interaction with distance occurs, there is a high coincidence of estimated curve with experimental data.

Great difficulties are encountered when efforts are made to interpret the effect of widening of acute angles on the basis of ordinary lateral inhibition [46]. Thus, ordinary lateral inhibition cannot explain widening of acute angles and narrowing of obtuse ones [53].

Inhibition between analogous primary detectors of local line tilt analyzers is confirmed on the neuronal level. In a study of neuronal mechanisms of simultaneous contrast, Blakemore et al. [54, 55] first investigated with a microelectrode reactions of a neuron selective for line tilt in the cat's visual cortex. When a grid of black and white stripes of optimal orientation (Figure 57a) was projected on the receptive field of such a detector, the neuronal reaction was maximal. Thereafter, the orientation of the grid remained constant throughout the experiment. Then the grid projected on the main receptive field was surrounded by a grid forming the inductive field. The experimenter changed the orientation of the grid on the inductive field at will. The purpose of the experiment was to examine the neuronal reaction as a function of correlation between grid tilt in the main and inductive fields. It was found that if the tilt of both grids coincided the neuronal reaction to the grid in the main field was almost entirely suppressed. With increase in difference between grid tilts, there was a decrease in inhibitory effect of the inductive field and it disappeared entirely with a difference of 45°. Further increase of the angle between grids led to appearance of excitatory effect of the inductive field, which first increased and then, as the angle between grids approached 90°, tended toward zero (Figure 57).

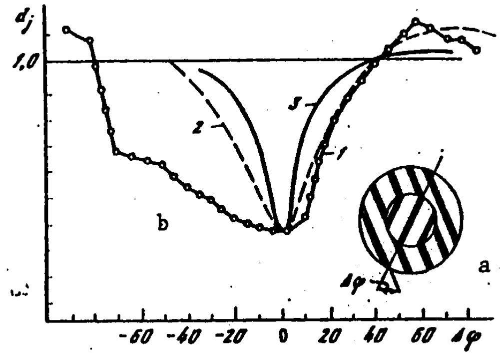

Figure 57. Effect of simultaneous contrast on the detector level

a) image of stimulus delivered to cat retina
b) detector reaction as a function of angle $\Delta\phi$
$\Delta\phi$) difference in orientation of grid angles in main and inductive fields
d_j) reaction of tested orientation detector
1) experimentally plotted curve for cat's cortical detector [54]
2, 3) functions calculated on model with following interaction coefficients: $\alpha = 0.2 \exp(-3 \sin \Delta\phi/2)$, $\alpha = 0.4 \exp(-4 \sin \Delta\phi)$

An analogous experiment can be reproduced with a secondary detector of the model of a line tilt analyzer. The response of the secondary detector to an optimally oriented line as a function of the line delivered to the input of the adjacent local analyzer was calculated on the assumption that inhibitory communications between analogous primary detectors depend on the distance between their receptive fields. The response calculated on the model coincides closely with the experimental data obtained from the study of a real neuron.

A number of authors (Blakemore et al., [56], Sekular et al. [57]) have tried to explain adaptation effects by means of usual lateral inhibition. Inhibition elicited by a preceding stimulus does not disappear right away, it does so gradually. As a result of inertia of the inhibitory process, it affects perception of the next stimulus, forming an aftereffect. To confirm this statement, Sekular [57] submits the results of an experiment, in which the subject was shown a stimulus in the form of a line with specific tilt for a short time (1 to 1000 ms) followed by delivery of the test line. The subject had to evaluate the tilt of the test line. It was found that perception of the test line changed with less than 30 ms intervals between stimuli. Subjectively, the test line seemed to be turned in the opposite direction from the inductive line, which corresponded to widening of the angle between lines. Since the time of delivery of the inductive stimulus was not sufficient to cause adaptation and the observed effect resembled the aftereffect observed with prolonged exposure of a stimulus, this aftereffect was interpreted as the consequence of inertia of lateral communications.

Simultaneous contrast and perceptive illusions in line tilt analyzer. The phenomenon of simultaneous contrast is based on inhibitory interaction between homonymous primary detectors. It can lead to a number of illusions of perception (Figure 58).

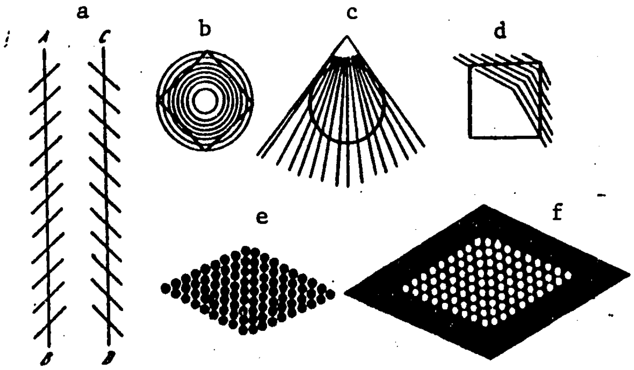

Figure 58. Examples of optical illusions based on interaction of different local sections of image outline

a) Zollner illusion (two parallel lines, AB and CD, on a background of non-parallel lines are perceived as not being parallel)
b) square on a background of circles is distorted
c) circle on a background of divergent lines is perceived as being flattened on the side of the acute angle
d) square on a background of nonparallel lines is significantly distorted
e, f) white circles on a black background and black circles on a white background are perceived as hexagons [47]

Zollner illusions: Two parallel lines on a background of two grids that are not parallel to one another are perceived by man as not being parallel.

The cause of this illusion is inhibitory interaction between homonymous primary detectors of different local orientation analyzers. As a result of interaction between parallel lines and background, they are subjectively turned in opposite directions: one line counterclockwise and the other clockwise. As a result, the objectively parallel lines are perceived as being divergent.

Other illusions can be explained in a similar way. Circles displayed to the subject are perceived as hexagons. This illusion can also be attributed to interaction between sections of outlines referable to different circles. As a result of inhibitory interaction between primary detectors, different segments of the circles are subjectively transformed to different degrees. The cause of dissimilar distortion of elements of the circle's outline is that the distances are different between interacting points of the outline. Each local segment of the outline therefore experiences a different inhibitory influence from adjacent segments, leading to dissimilar distortion of the outline of the circle. As a result, man perceives circles as hexagons.

Poggendorff illusion: This illusion (Figure 59) consists of perceiving segments of one line intersecting two others as segments of two different lines shifted in the vertical plane. At the same time, segments belonging to different lines are perceived as belonging to one line.

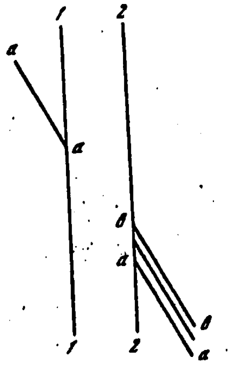

Figure 59.
Poggendorff illusion

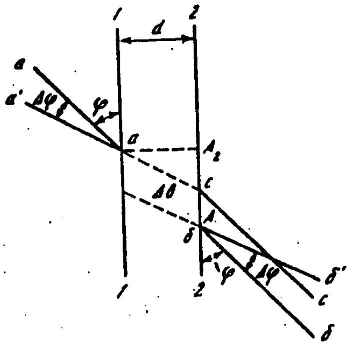

Figure 60.
Explanation of Poggendorff illusion

Thus, segments a-a and a-a are segments of the same line, although subjectively they are perceived as being shifted from one another.

The explanation of the Poggendorff illusion is based on a mechanism of inhibition of the "simultaneous contrast" type. As a result of interaction with the lines, the segments are subjectively turned counterclockwise and perceived as belonging to different lines (Figure 60).

Segments a-a and b-b belong to the same line. As a result of interaction with lines 1-1 and 2-2, segments a-a and b-b are perceived to be rotated counterclockwise by an angle $\Delta\phi$, consequently, as segments a-a' and b-b'. For this reason, segments a-a and b-b are no longer perceived as the continuation of the same line: they appear to be shifted from another by $\Delta\delta = AA_2-CA_2$. However, segments a-a and c-c are subjectively perceived as belonging to the same line.

The subjective shift as a function of angle between line segments was calculated on the model (Figure 61). In the calculation, the function of widening of an acute angle was used (Appendix 4).

Masking phenomenon: Excitation and inhibition do not disappear instantly after discontinuing a stimulus; this occurs gradually, with some lag. For this reason, with successive delivery of two stimuli, the excitatory and inhibitiory processes elicited by them are superimposed, so that each of the two stimuli affects perception of the other. This is known as the "masking effect" of one stimulus on another [58].

Both summation of excitatory processes in one local analyzer and inhibition via inhibitory connections between homonymous detectors of different local analyzers are involved in masking of one stimulus by another.

Interaction of excitations leads to the effect of mixture of line tilts, causing two stimuli to merge into one. It is difficult to correctly assess the test stimulus since, by virtue of inertia of processes in neuronal nets, excitation elicited by a stimulus is summated with excitation from the preceding (direct masking) or next stimulus (backward masking), generating the subjective perception of a line with an intermediate tilt.

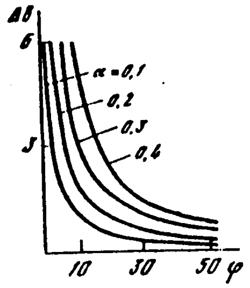

Figure 61.
Vertical shift Δb as a function of angle ϕ (designations are the same as in Figure 62)
α) interaction coefficient

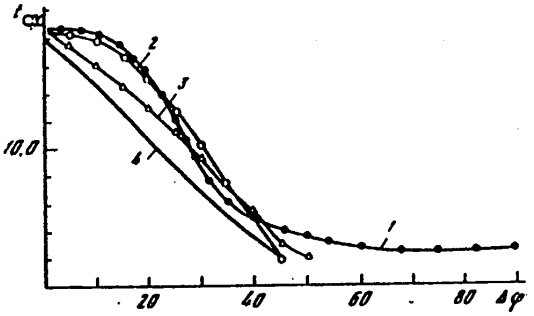

Figure 62.
Masking phenomenon
ϕ) angle between test and masking lines
t_{cr}) minimum required duration of test stimulus for perception
1) experimentally established function for man [60]
2,3,4) functions calculated on model with different interaction coefficients

Inertia of inhibitory processes also affects the process of development of excitation elicited by stimuli. Maximum inhibitory interaction between stimuli is obtained when the tilt of the test and masking lines is the same (Appendix 4). The method of calculating the effects of inhibition is based on the assumption that, for proper perception of the tilt of a test stimulus the output detector coding this line tilt must be exicted for a certain fixed time. Inhibition by the masking stimulus affects the time, during which the detector is excited above the threshold level. The masking line inhibits activity of the test line detector if the angle between them is less than 45°. If the angle is greater than 45°, the masking line has an excitatory effect on detector activity (Appendix 4).

Meyer et al. [59] demonstrated that the duration of a test stimulus in the form of a black and white grid is perceived as being shorter if the orientation of the masking stimulus coincides with the orientation of this grid. If, however, the stimuli are orthogonal, the apparent duration of the test stimulus is increased.

Minimum duration of test stimulus required for perception as a function of angle between test and masking lines, which was calculated on the model, coincides with the response obtained by Sekular et al. [60] in direct experiments on man (Figure 62).

Matin [61] and Abadi [62] also report a close correlation between the masking effect and inhibitory mechanism of simultaneous contrast. The outline of an object is represented by detectors of segments with a specific tilt as a result of the activity of the set of local analyzers of line orientation. The distinguished outline segments can then be combined into outline segments of different length and orientation.

CHAPTER 6. VISUAL ANALYZER OF DIRECTION AND SPEED OF MOTION

Principles of coding direction and speed of motion. A special system of neurons referable to the Y or W type is used to code moving optical stimuli. The distinction of these neurons is that they respond with a rapidly fading discharge to stimulation with a stationary stimulus. The neurons that code motion can be subdivided into three major groups: those coding direction of motion, coding speed of motion and those that are selective to both speed and direction of stimulus motion.

Neurons that are sensitive only to motion of a stimulus for the mechanism of perception of motion regardless of other features of a moving object [63]. Thus, there is an independent motion analyzer in the visual system of man and animals.

Does the motion analyzer have features of the previously discussed "standard analyzer"?

In a survey article dealing with neuronal mechanisms of coding motion, Grusser [64] distinguishes five types of neurons reacting to movement of a visual stimulus. Among the distinguished neurons, direction-selective neurons occupy a special place, and they are responsible for coding direction of movement.

Neurons have also been found that react selectively to the speed of movement of an object [65, 66].

Thus, there are at least two independent analyzers in the nervous system of man and animals: analyzer of direction and analyzer of speed of motion.

Direction-selective neurons and analyzer of direction of motion: These neurons are encountered on different levels of the visual system, ranging from the retina to the visual cortex [64]. The neurons found on the lower levels of the visual analyzer may be primary detectors.

Best studied are the direction-selective neurons of the rabbit retina [66, 67]. Their reactions depend on the direction of movement of a point stimulus. The direction of stimulus motion with which a given neuron is maximally excited is generally called optimal. The direction with which the reaction of a given neuron is minimal is called zero direction. The neurons separate into four groups, the optimum directions of which form an angle of 90° with one another [68, 66]. Analogous distribution of neurons according to optimum direction has been found in the superior colliculus of the cat.

The characteristics of neuronal responses to change in direction of stimulus motion are described by cosine curves, the argument of which is the angle of direction of motion of a point stimulus. A deviation from a cosine curve is observed only with directions that are quite far from optimal [67, 69] (Figure 63).

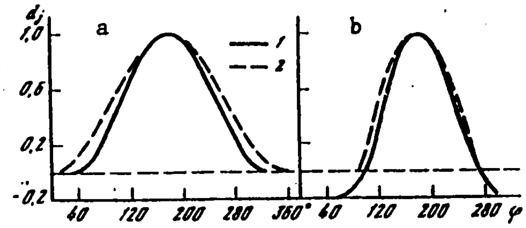

Figure 63. Characteristics of sensitivity of direction-selective neurons in the rabbit

- ϕ) direction of movement of point stimulus
- d_j) level of neuronal excitation
- 1) curve of neuronal reaction of rabbit retina (a) [67] and lateral geniculate body [69] (b)
- 2) theoretical functions of sensitivity of primary detectors of motion direction

This enables us to assume that direction-selective neurons perform the functions of primary detectors of motion direction. There are four primary detectors, because each of them effects only the positive part of the response.

Secondary detectors of direction of motion: In the rabbit and cat visual cortex, direction-selective neurons often have different optimal directions of motion [70-73]. It can be stated that there is "reproduction" of detectors on higher levels of the visual system, which are selective to direction of motion of a visual stimulus. According to Creutzfeldt [45], the selective responses of cortical detectors of direction of motion in the cat are effected only by two or four neurons of the lateral geniculate body. This can be explained on the assumption that the neurons of the lateral geniculate body are primary detectors of direction of motion, while the selective neurons of the visual cortex are secondary detectors.

On the basis of these data, it can be concluded that the structure of the analyzer of direction of motion conforms to the general principles of construction of analyzer systems. The analyzer of motion direction contains neurons with the properties of primary detectors. On higher levels of the visual system, there is "reproduction" of detectors, which cover all directions of movement. Their properties are those of secondary detectors in the standard analyzer model.

Model of visual analyzer of direction of motion. The model of the analyzer of motion direction consists of the following layers: receptors, primary detectors and secondary detectors. A stimulus moving over the receptive field excites primary detectors which, in turn, excite secondary detectors. As a result of the special organization of communications between primary and secondary detectors, one of the latter is found to be more excited than the others. The number of the secondary detector with maximal excitation determines the direction of movement "perceived" by the model (the structure of the model is illustrated in Figure 64).

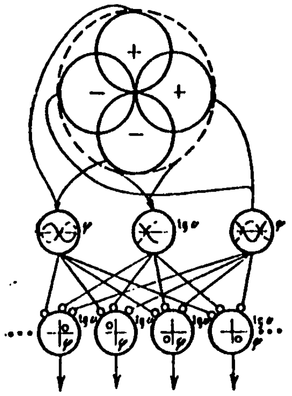

Figure 64.
Structure of spherical model of visual analyzer of direction

The local receptive field of the retina services several primary detectors: four orthogonal primary detectors of direction and detectors of speed of motion. An object moving at a certain speed over a certain trajectory in the local receptive field of the retina generates a three-component excitation vector. The four detectors of direction work in pairs. A pair of primary speed detectors is added to them. The solid line illustrates the response of the detectors in the form of sin ϕ or cos ϕ, and the dash line in the form of sin (ϕ + 180°) and cos (ϕ + 180°). The excitation vector acts through the fan of communication vectors on the secondary detectors, creating maximal excitation on one of them. Thus, the speed and direction of movement are recoded into the number of the channel with maximum excitation.

Primary detectors of model of analyzer of motion direction: According to the foregoing, successive illumination by point stimuli of receptors situated along a specific trajectory is sufficient to excite a primary detector. There must be some lag in illumination of different receptors, which corresponds to the time required to shift the stimulus from one receptor to another with ordinary movement.

This property of the detector of direction of motion was demonstrated in the chipmunk retina [74]. Apparently, the same mechanism is reponsible for the illusion of movement, or phi phenomenon, in man. If short flashes are used to illuminate two points on a screen successively, with a properly selected lag, the subject sees smooth movement from one point to the other [75, 76]. Selective stimulation of the analyzer of direction of motion is the cause of the phi phenomenon.

Construction of secondary detectors of motion direction: The secondary detectors are constructed in the standard way: a communication vector is selected for each secondary detector that is collinear to the excitation vector induced by the stimulus for which this detector must be adjusted. The modulus of the communication vector is a constant, and it is unrelated to the detector number. There is a one to one correspondence between the number of the output detector with maximum excitation and direction of excitation vector.

Differential sensitivity of the model is determined by the magnitude of change in direction of object movement that must be made so that maximal excitation would shift from a given secondary detector to the one closest to it. Two is the least number of primary detectors. Their responses are given by the sine and cosine curves of the angle of direction of movement of the stimulus in relation to the selected system of coordinates. The moving stimulus excites primary detectors, determining the value of components of the excitation vector. There is one to one correspondence between the direction of the excitation stimulus and direction of stimulus movement. The direction of movement of the stimulus and excitation vector can have any value from 0 to 360°. The proposed coding method is equivalent to the reflection of the physical space of motion direction in perceptive space in the case where subjective differences between stimuli equal their objective differences.

The receptive fields of primary detectors of the analyzer of direction of motion can be constructed in different ways. One of them consists of the following: each light-sensitive element of the receptive field sends a signal to a primary detector via two channels--inhibitory and excitatory. The speed of signal transmission is different in the two channels, and it depends on the location of the receptors. If the stimulus moves in the optimum direction, the signals from photoreceptors are summated, and the signal at the input of the primary detector is maximal. If the signal moves in the opposite direction, the inhibitory signal suppresses the excitatory signal entirely. In this case, the signal at the input of the primary detectors becomes minimal. When the stimulus moves in intermediate directions there is only partial suppression of the excitatory signal. One can so choose interaction between excitatory and inhibitory processes that the resultant signal of the primary detector will equal the sine and cosine of the angle of direction of stimulus movement. Differential sensitivity of the analyzer of motion direction depends on the direction of movement. The number of cortical detectors that code vertical or horizontal movement of an object is greater than the number of detectors that code diagonal directions of motion. This corresponds to a difference in detector density: differential sensitivity is greater for vertical and horizontal movements than diagonal [72].

Adaptation effects in the visual analyzer of direction of motion. This analyzer is analogous in many respects to the analyzer of line tilt. The only difference is that the sensitivity characteristics of primary detectors of the analyzer of direction of motion are represented by the cosine and sine of the directional angle of motion, while those of primary detectors of the orientation analyzer are represented by the sine and cosine of the double angle of line tilt. In the case of the analyzer of direction of motion, the distance between stimuli in physical and perceptive space coincide, whereas in the orientation analyzer the distance is twice as long in subjective space as it is in physical space.

The effects of adaptation have the same appearance in the model of the analyzer of movement direction as in the model of line orientation analyzer. However, all angles between directions that are not subject to adaptation are twice the size of the corresponding angles in the model of the line orientation analyzer.

If the optimum trajectories of receptive fields of primary detectors are superimposed over the coordinate axes, movements at angles of 45, 135, 225 and 315° will be stable directions, while those at 0, 90, 180 and 270° will be unstable.

However, psychophysical experiments have shown that 0, 90, 180 and 270° are stable directions [78].

For vertical or horizontal directions of motion in the model not to undergo adaptation, the receptive fields of primary detectors on the retina must be so oriented as to have their optimum directions turned by an angle of 45° in relation to the vertical of the gravity field. Then prolonged viewing of an object moving in any of the directions of 0, 90, 180 and 270° does not affect subsequent perception of motion.

Normalization effect when man views for a long time a point stimulus moving in a specified direction: Experiments conducted to study the normalization effect in the human analyzer of direction of motion provide an answer to the question of whether there is a change in perception of direction of motion during prolonged viewing of a moving stimulus.

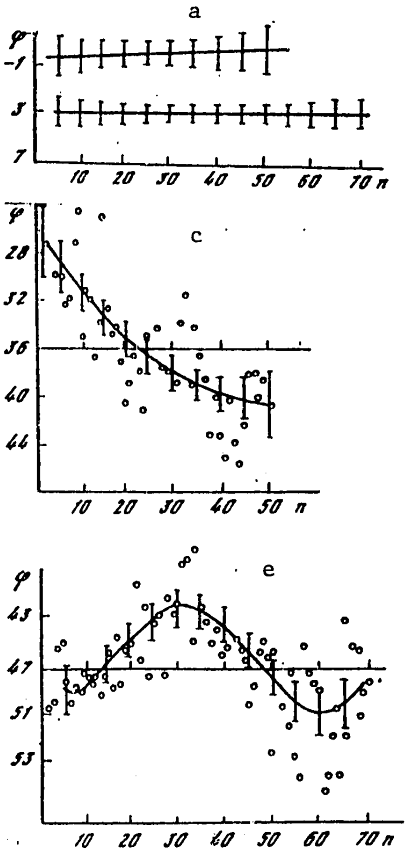

Figure 65. Normalization effect in human analyzer of direction of motion

n) sequential number of setting required direction in successive setting by subject of specified direction of motion of a point stimulus

ϕ) direction of movement of illuminated point set by subject

a) specified direction of movement

a) $\phi = 0°$

b) $\phi = 90°$

c) $\phi = 28°$

d) $\phi = 51°$

e) $\phi = 45°$

A spot of light was shown to the subject in total darkness; it moved from the center to the periphery of a television screen. The speed of movement of the point over the screen was constant throughout the experiment. The subject had to set the movement of the point in a previously specified direction 50-70 times in a row, by controlling the voltage. It was assumed that with each successive setting of specified direction the result of each prior setting would affect the next one, since the subject tried to set a direction of movement that would not differ from the preceding one subjectively, and there could be accumulation of systematic error from setting to setting.

If the subject was required to set vertical or horizontal direction of movement, there was virtually no change in error of specified direction from test to test (Figure 65, a, b).

If, however, the subject was asked to set one of the tilted directions at an angle of 26 or 50°, the magnitude of error increased from trial to trial. With an angle of 26°, the subject set a direction of movement that deviated more and more from vertical (Figure 65c) and with an angle of 50°, it deviated more and more from horizontal (Figure 65d). In both cases, there was a tendency to choose directions that were closer to diagonal. This was manifested by constant drift of perceived direction toward the diagonal. The cause of the drift was that, when viewing a moving point, the primary detectors of direction of movement were perceived, under the influence of adaptation, as being more and more vertical (with an angle of 26°) or more and more horizontal (with an angle of 50°) (Appendix 4).

In order to reproduce the standard, the subject altered the trajectory of movement, shifting it from vertical or horizontal. As a result, the trajectory of movement approximated the diagonal from setting to setting. The closer the set direction of movement of the spot was to a diagonal, the less drift there was. If, however, the subject crossed the boundary formed by diagonal direction, drift changed to the opposite direction. This can be seen from the results of an experiment, where the subject was asked to set close to diagonal directions of spot movement (Figure 65e).

If the receptive fields of primary detectors are so oriented in the retina that their optimum axes are rotated by 45° in relation to the gravity vertical, the diagonal direction of movement is unstable: a deviation from it generates drift of settings toward the closest stable direction [77].

When the subject was asked to set an unstable direction, there was usually continuous increase in setting error. When setting a strictly diagonal direction of movement, the error fluctuated about the specified direction. In this case, the constant reversal of the sign of adaptation drift prevented accumulation of error.

Aftereffect in perception of direction of motion: In the proposed model of an analyzer of movement direction, the aftereffect has the same appearance as in the model of the line orientation analyzer. The only difference is that the aftereffect response for direction of movement is doubled along the x-axis, in relation to angle.

Studies have been made of the effect of prior adaptation to a stimulus moving in a specified direction on subsequent perception of vertical movement.[78, 77]. When the trajectory of the test stimulus was turned clockwise the error was considered positive, otherwise negative.

It was found that when the angle between the specified direction of movement of the adaptive stimulus and gravity vertical was less than 90° there was a positive aftereffect. When, however, this angle was larger than 90°, a negative aftereffect was observed (Figure 66).

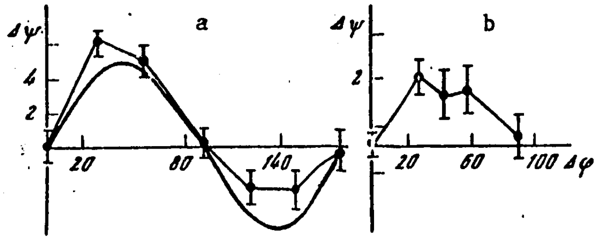

Figure 66. Aftereffect in analyzer of direction of motion

φ) angle between direction of movement of adaptive stimulus and vertical direction of movement from bottom to top
Δψ) systematic error in setting vertical direction of movement
a,b) aftereffect in different subjects (each point on the curve is the mean of 10 settings; the vertical segment defines the 99% confidence interval)

The results of this experiment show that the observed effects are the consequence of adaptation in expressly the motion direction analyzer, rather than a side-effect of adaptation in the line orientation analyzer. This is proven by the effect that normalization effects and aftereffects are characterized by other angles in the analyzer of direction of movement than would be expected for the analyzer of line tilt.

Thus, prior adaptation to movement of the point in directions at angles of 0, 90 and 180° does not affect subsequent perception in the analyzer of motion direction of the vertical direction of movement of the test stimulus. In the line tilt analyzer, prior adaptation to lines tilted at angles of 0, 45 and 90° from the vertical does not affect perception of the vertical. While lines tilted at angles of 0°, 22°30', 45°, 67°30' and 90° are perceived in the line tilt analyzer as constant when viewed for a long time, in the analyzer of direction of motion stable directions are those oriented at angles of 0, 45, 90, 135 and 180°.

The adaptation effects are identical in the real analyzer of direction of motion and its model. In both cases, the functional significance of adaptation is that the discriminating capacity of the system increases. This is achieved by a change in responses of primary detectors in accordance with the excitation level they reach. Such attenuation of neuronal reactions in the cat's visual analyzer under the effect of a prolonged moving stimulus apparently reflects the process of adaptation of primary detectors [79].

Simultaneous contrast in visual analyzer of direction of motion. Simultaneous contrast is provided in the motion analyzer by inhibitory connections between homonymous primary detectors representing different sections of the visual field. If the angle between trajectories of movement is less than 180°, there is an increase in difference in perception of direction of movement of two stimuli moving in different sections of the visual field. If the angle between the two directions is greater than 180°, there is a decrease in subjective difference between the directions of movement of these stimuli.

Michael [80], who made a study of the properties of visual system neurons of the ground squirrel that detect the direction of motion, observed that the reaction of such a neuron depends not only on movement of the stimulus in the neuron's receptive field, but on the direction of movement of a stimulus delivered beyond its receptive field. If the direction of movement of both stimuli is the same, there is virtually complete suppression of neuronal activity. If, however, the stimuli move in opposite directions, there is no change in reaction of the tested detector. Thus, it can be concluded that two stimuli inhibit one another the most when they move in the same direction. If the stimuli shift in opposite directions, there is no inhibitory interaction. The inhibitory connections between homonymous primary detectors placed in the model reproduce this phenomenon.

With simultaneous movement of two stimuli in the receptive field of one local analyzer of movement direction, their combined effect cannot be distinguished from the effect of one stimulus moving in an intermediate direction. In both cases, the number of the output detector with maximum excitation is the same. However, the amplitude of detector excitation will depend on the angle between directions of movement of these stimuli. The larger the angle, the lower the level of excitation of the detector. When the two stimuli move in opposite directions, the amplitude of detector excitation equals zero: the stimuli suppress one another entirely. It was experimentally demonstrated that there is mutual suppression of two stimuli moving in opposite directions in the receptive field of the ground squirrel's detector.

Analyzer of speed of motion. The model of this analyzer can be constructed of neuron-like elements by the standard method. The sensitivity characteristics of primary detectors of speed of movement must be represented by sine and cosine functions. Then, when the speed of movement is increased the response of one primary detector diminishes and that of the other increases. Different methods can be used to organize the receptive field of primary detectors of speed of motion.

However, if we accept the principle of organization of the receptive field of the analyzer of direction of motion, by using a different lag between excitatory and inhibitory inputs one can render the primary detector sensitive to speed of movement of an object. Neurons that are selectively sensitive to speed of motion, but not selective for direction of motion, can perform the role of primary detectors.

However, direction-selective neurons are also sensitive to speed of motion: some react to low speeds of stimulus movement and others to high speeds. The sensitivity characteristics of direction-selective neurons to speed of motion of a stimulus correspond well to the characteristics of cone sensitivity described by the Dartnell nomogram. One can construct speed-selective secondary detectors that are also selective for direction of motion on the basis of primary detectors with sensitivity in the form of Dartnell nomograms.

If the primary detectors are constructed on the basis of direction-selective neurons (Appendix 5), concurrent contrast will depend not only on the difference in speeds of delivered stimuli, but difference in direction of their movement.

Adaptation of primary detectors of the speed analyzer leads to the normalization effect, which consists of the fact that, when viewing a stimulus for a long time, its speed changes slowly, but continuously, coming close to the speed that corresponds to equal excitation of both primary detectors. This speed will be the invariant speed of stimulus movement. In the course of adaptation any stimulus speed that is slower than the invariant level will subjectively increase and one that is faster will monotonously decrease, striving toward the stable invariant value.

Prior adaptation to one speed of motion elicits changes in perception of speed of the next stimulus. If one selects as the adaptive speed one that is less than the invariant speed and as the test stimulus one that has the invariant speed of movement, subjectively there will be an increase in speed of the test stimulus. Conversely, the speed of the test stimulus will diminish if it is preceded by an adaptive stimulus that is faster than the invariant speed.

Such aftereffects exist in the human analyzer of speed of movement [81].

Simultaneous contrast in the speed analyzer is provided by addition of inhibitory connections between homonymous primary detectors of different local analyzers of movement speed. As a result, the subjective difference between stimuli increases. This is associated with seeming slowing of low speeds and seeming acceleration of faster movement of the stimulus. Thus, simultaneous contrast acts in the direction that emphasizes differences.

Simultaneous contrast has been demonstrated in the human analyzer of velocity [82]. Along with increasing differential sensitivity, simultaneous contrast renders perception of velocity of a stimulus relatively independent of speed of motion of the background against which the object is moving.

Indeed, background signals acting on primary detectors of the set of local speed analyzers are mutually suppressed.

Spherical model of visual analyzer of motion. Are the direction and velocity analyzers independent analyzers, or are we dealing with two aspects of function of the same visual analyzer? It was learned that there is a specific combination of direction and speed of an optimum stimulus for different neurons, with which a particular neuron exhibits a maximum response. With optimum velocity there is the greatest directional selectivity. At the same time, with optimum direction of stimulus movement, there is maximum selectivity with respect to speed.

It can be assumed that signals from three types of primary detectors converge on such secondary detectors that are selective for a specific combination of velocity and direction of movement. Two types of primary detectors determine selectivity for direction, while the third type of primary detectors gradually reacts to speed of movement of an object.

Excitation of the three types of primary detectors constitutes three coordinates in Euclidean space. Thus, there is one to one correspondence of an optical stimulus moving in a specific direction and at a specific speed with a three-component excitation vector of primary detectors.

The secondary detector with a collinear vector of communication with primary detectors will be selectively excited when a stimulus is delivered to its receptive field that has motion parameters generating such a three-component excitation vector.

The perceptive field of the visual analyzer of motion is illustrated in Figure 67.

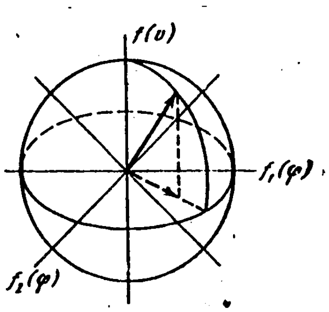

Figure 67.
Spherical model of visual motion analyzer

Excitation of primary detectors of direction of motion $f_1(\phi)$, $f_2(\phi)$, which provide for perception of signals in the four quadrants of the equatorial plane, as well as excitation of primary velocity detectors $f(v)$, are plotted on the three axes of the perceptive space of motion perception. The X and Y axes are shifted by 45° in relation to the gravity vector. An object moving in the visual field has a certain direction and velocity. This leads to excitation of the three primary detectors in a certain combination. The secondary detectors are selective to specific combinations of excitation of primary detectors due to selection of connections that are collinear to the excitation vector of primary detectors. The secondary detector is selectively excited with a specific combination of velocity and direction because of this arrangement. Thus, different points on the sphere correspond to secondary detectors with maximum excitation. When the direction is fixed, a change in velocity leads to shifting of excitation maximum on the meridian. Direction detectors that are selectively adjusted for optimum speed are situated on the equator. Detectors that code slowly and rapidly moving objects are located at the poles.

Since each secondary detector satisfies the sphere equation, the entire set of secondary detectors is located on the surface of the sphere that forms a quasireceptive surface. Subjective differences between stimuli are determined by the distances on the small arc of the large circle, as in the spherical model of the color analyzer.

For the final construction of the spherical model, one must properly determine the position of the axes in relation to fixed parameters of motion. The primary detectors of direction of movement must be turned by 45° in relation to the gravity vector. In turn, zero velocity and maximum velocity, when direction of motion loses meaning, should be placed on the poles (Figure 67).

Neurons that are adjusted for optimum speed, at which the responses of gradual detectors of high and low speeds equal zero, will lie on the equator. The contribution of primary detectors of direction of movement also equals zero at the poles. The main effect is reproduced in the model: selective reactivity of motion detectors for a specific combination of velocity and direction of movement.

CHAPTER 7. STEREO ANALYZER

Neuronal mechanisms of stereopsis. With the joint function of both eyes, the orientation of the line of vision is usually so selected as to have the viewed object projected in the foveal part of the retina. The point in space where the lines of vision of both eyes intersect is called the point of fixation. Thus, an object located at the point of fixation is projected on the central part of the retina. All other spatial objects are visible at a certain angle in relation to the point of fixation. The distance on the retina between projections of the point of fixation and an arbitrary point in three-dimensional space can be described as the angle of vision. The difference between angles of vision of an arbitrary object of the left and right eye is usually called disparity. It is assumed that disparity is used to determine the position of an object in three-dimensional space in relation to the point of fixation [83, 84].

Studies of the cat and monkey visual cortex revealed a population of neurons that undergo maximum excitation only when a stimulus is localized in a specific point in space [85-87]. Separate stimulation of each eye does not elicit neuronal reactions. Excessive disparity of stimuli to both retinas, as well as insufficient disparity, lead to inhibition of the neuronal response. The response of a binocular stereoneuron is selectively enhanced only when there is a specific magnitude of disparity of the image on the retina. One can find a specific disparity of stimulus for each binocular stereoneuron. A shift of signals in relation to the center of the retina corresponds to a specific direction in space, while each specific disparity corresponds to a specific distance of the stimulus. In other words, each binocular stereoneuron is specific for a certain direction to the object and its specific distance. It is assumed, that the eyes fix on the same point. This means that the direction and distance of objects are coded by means of stereoneurons in relation to a specified point of fixation. All of the foregoing applies to points in the horizontal plane.

Thus, there is a set of detector neurons for perception of an aggregate of points in external space in the horizontal plane, each of which responds only to a specific combination of direction and distance. This set of stereodetectors forms a quasi-receptive surface, the so-called internal cyclopian screen on which the position of the points is reflected. When the points come closer, farther or change in direction, the excitation maximum shifts over the cyclopian set of stereodetectors. Consequently, a certain combination of excitations of the two retinas is transformed into a single excitation of a specific stereodetector.

If we were to apply analogous reasoning to points that are not in the horizontal plane of external space, but in the plane that forms a certain angle with the horizontal plane, a quasireceptive surface formed by its own stereodetectors can be formed for each such plane. As a result, there is a set of quasireceptive surfaces representing the entire diversity of points in external space. This stereodetector space forms internal cyclopian space: signals from both retinas are transformed in it into a single excitation corresponding to the given direction, distance and height of a point. It can be said that, for each element of one retina there is an element or group of similar elements in the other retina, joint stimulation of which leads to selective excitation of a specific stereodetector, with which there is fusion of images into a single stereoscopic image.

The region of external space in which two images can merge into a single stereoscopic image is named after the researcher of the effect of stereoscopic fusion--Panum's area. Beyond Panum's area there are double images. In the language of detector description, this means that there are some restrictions imposed on disparity. When disparity exceeds the magnitude expressed by the set of disparities of receptive fields fusion is impossible. Thus, Panum's area is represented by a set of detectors that differ in selectivity for magnitude of disparity of retinal receptive fields. Each direction in external space is represented by its own set of stereodetectors with different disparity of receptive fields. The term, "disparity of receptive fields," refers to the necessary magnitude of divergence of receptive fields on each retina to obtain a maximum response by the stereodetector. The possible disparity of receptive fields increases from the center to the periphery of the retina. For this reason, Panum's area is wider for directions that are far from the center. Thus, there is a gauge of stereodetectors with different disparities of receptive fields for each of the directions considered, which code by channel number the relative distance in a given direction. On the other hand, there is a set of stereodetectors for a specific distance in different directions, to which different directions at the given distance correspond. There is a mechanism of separation of space into planes to represent points in three-dimensional space: detectors with the same disparity of receptive fields for different directions and different deviations from the horizontal plane distinguish in the external space the plane [layout] whose points are perceived as being at the same distance from the observer.

The cyclopian space formed by the set of stereodetectors is made up of neurons of the 17th field of the visual cortex and it is aconstant in the sense that when the line of vision shifts the focus of excitation shifts in accordance with the shift of the image of the point on each retina. However, human stereoscopic perception is constant: points in external space are perceived with retention of their position, in spite of the shift of their images on the retinas with eye movement. One must take into consideration the principles of coding eye position in order to identify the neuronal mechanism of constancy.

Neuronal mechanisms of coding position of line of vision. There must be a mechanism that considers eye position to assurace constancy of spatial perception. The position of the line of vision in the nervous system is also based on the principle of signal coding by channel number.

In total darkness, when the effect of photic stimuli is ruled out entirely, one can detect the neuronal mechanism of coding viewing position. The detectors of position of line of vision are afferent neurons which are excited when the eyes occupy a specific position in relation to the orbits.

If the line of vision shifts, excitation maximum shifts from one detector to another. The detector is excited for the entire time that the line of vision occupies the specific position for this detector. Such coding has been established for shifts of line of vision in the horizontal plane. The question of coding of height of line vision in relation to the horizontal plane remains open. However, if we consider the general principle of coding by channel number, the principle of selective detectors should also be used to code the position of line of vision in relation to the horizontal plane. A shift of line of vision in depth requires conjugated convergence or divergence of the eyes. There are data indicating that there is an independent set of selective detectors to code vergence of vision. Considering the coding of vision when the eyes are turned, shifted in relation to the horizontal plane and in vergence, it can be stated that all of the external space represented by points on which vision can be fixed is coded by a combination of detectors of position of line of vision. If the line of vision shifts, excitation maximum shifts over the sets of detectors. Construction of detectors of position of line of vision is the same as construction of detectors of intensity: signals from the proprioceptor muscles of the eyes travel to primary detectors of which are built detectors that are selective for specific combinations of proprioceptive signals. However, there is also another way of obtaining information about the position of the eyes, which makes use of a copy of the command that serves to shift the eyes to a specific point. These signals may be impulses from command neurons that control direction of vision.

Constancy of spatial perception. Thus far, all efforts to find stereodetectors in the visual cortex that would be invariant in relation to eye position have failed. But the neurons in the parietal region, which is characterized by interaction of analyzers of different modality in construction of the human body schema, retain the localization of their receptive field in space with different position of line of vision. This corresponds to the conception of properties of constant reflection of the external environment on a population of invariant detectors. This constant space of stereodetectors differs basically from cyclopian aconstant space in that the receptive fields are not determined by the position of the stimulus on the retinas, but by the objective position of the stimulus in external space. Since we have no data as yet concerning the principles of neuronal realization of constant coding, we have to construct a model and then test its conformity to psychophysical data obtained from studies of stereoscopic vision in man. General theory of invariant detectors, as detectors with adjustable communication vector, is the starting point for building such a model. The communication vector changes under the influence of signals from detectors of another modality.

Model of depth analyzer. Main premises used in building the model. The abovementioned model, which is based on certain experimental facts, has flaws along with a number of positive properties, such as simplicity of explaining mechanisms of stereoscopic fusion; these flaws ensue from the desire to combine in one model both the mechanism of image fusion and the mechanism of depth coding. A number of difficulties arise when one tries to use it to explain some experimental data.

1. Object vision may be absent with the sensation of depth. Thus, if images on the left and right retinas consist of randomly scattered points differing in brightness and chromaticity, when they are appropriately chosen the sensation arises that part of the image is farther or closer than the point of fixation [88-90]. Images on the left and right retinas consist of randomly scattered points or spots, in

which there is no consistent structure in the form of specifically oriented lines when viewed separately. If we consider that the disparity detectors found in the cat's visual cortex are organized, according to Bishop [87], on the basis of superposition of two monocular detectors of a line with one orientation, appearance of depth perception when there is an image on each retina in the form of randomly scattered points is incomprehensible.

2. Depth perception in diplopia [91] is also not explained satisfactorily in this model. If the mechanism of depth perception is the same with diplopia and fusion of monocular images, the above-described model is a model of stereoscopic fusion of images, and not a model of the mechanism of depth perception.

3. When two stimuli are delivered to a subject, in the presence of summation depth perception occurs as the mean of the sum of depths of each stimulus. By changing the intensity of a stimulus one can alter the contribution of this stimulus to evaluation of the resultant depth [16]. This phenomenon is known as the depth mixing phenomena. In the model under discussion, the phenomenon of depth mixture is not explained.

All this warrants the belief that there is an independent depth analyzer in the nervous system to measure depth. The process of fusion of images is an independnet process.

If there is no need for objective organization of images delivered separately to each retina for occurrence of depth perception, the depth feature is distinguished in the visual analyzer independently of objective [object] vision. This statement is consistent with the fact that the time required for occurrence of depth perception is shorter, or at least not longer, than the time required for object perception [84].

It must be stressed that any model of a stereo analyzer must provide for monocular perception of object direction even without perception of this object in depth.

Let there be two light-sensitive retina-matrices spread in space horizontally by the magnitude formed by interocular distance. Each of the photomatrices can turn independently of one another about a certain point called the central point of the retina. Moreover, the matrices can also make coordinated turns about this point. Signals about the magnitude of rotation of the retinas in the vertical and horizontal planes are coded by neuron number by means of three systems of primary detectors: those formed by receptors of the muscles of one eye that turn it in the horizontal plane; those formed by proprioceptors of the same muscles of different eyes, turning the eyes in the horizontal plane. The detectors of signals from muscles that turn the eyes up and down in relation to the horizontal plane code the position of the line of vision in the vertical plane.

The photomatrices have an optical system for automatic focusing of an image in the matrix (retina) plane. In addition, the optical axes are orthogonal to the retinal plane and traverse the centers of the retinas (see Figure 68). In Figure 68, point of fixation *1* is on the Fit-Muller circumference. It is projected in the center of the receptive fields of the right and left eye. These points are marked on the retina of each eye with an "x". Their receptive fields are characterized by zero disparity; the position of the centers of the receptive fields euqals zero in relation to the central direction. Point *2* in the other direction lies on the horopter and is projected on receptive fields whose centers *2'* have disparity that equals the difference between their projections on the retina. The angle between the center of the receptive field and projections of point *3* on the retina is characterized by relative disparity within the receptive field--difference between angles α and β. The position of the projection of an arbitrary point on the retina can be given unambiguously by means of two pairs of angles, α and γ, β and δ. Angle α determines the angle of vision by the left eye of point Δ in the horizontal plane, in relation to the main optical axis, while γ determines the vertical angle. Angles β and δ set the position of the projection of point Δ on the other retina. Thus, the two pairs of vertical and horizontal angles are independent physical variables that characterize the position of point Δ in space, in relation to the given orientation of the eyes.

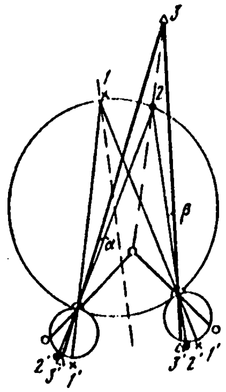

Figure 68.
Diagram of projection on the retina of both eyes of points situated at different depths in relation to the fixation point

If the optical axes intersect in space, we shall call this point fixation point Φ. Then angles α, γ and β, δ are defined in relation to the given fixation point.

According to the foregoing, all measurements taken in the stereo analyzer are relative--the fixation point is the reference center. Perception of absolute distance is possible only if there is an additional system that codes the position of line of vision or position of fixation point in space.

Description of model: According to the "standard model" of a sensory analyzer, any physical feature of a stimulus is coded by the direction of the excitation vector. The dimensionality of the vector is determined by the number of independent primary detectors. The responses of these detectors to the coded feature must satisfy the general requirements of maximum integral sensitivity of the system as a whole. In turn, the direction of the excitation vector is coded with the number of the output element, called secondary detector, which has maximum excitation.

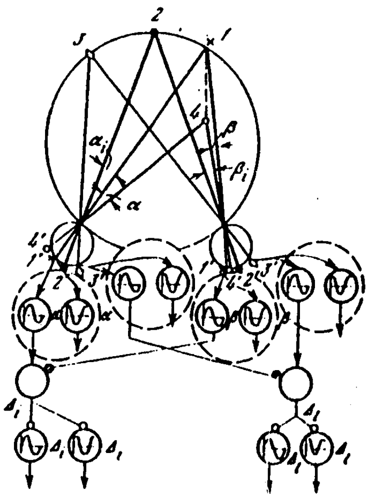

Figure 69.
Structure of local depth analyzer

When perceiving an object, there are two pairs of angles for each eye, at which it is seen monocularly. If the angles of vision are coded in a separate analyzer, the number of independent primary detectors for each eye is four. Detector neurons for angular size may be used as such detectors [92, 93] (or ordinary neurons with concentric on-off fields). The sensitivity characteristics of these detectors are described by the cosine or sine of the corresponding angle of vision (Appendix 6). The level of detector excitation determines the values of components of excitation vectors. Each excitation vector codes the angle at which an object is seen monocularly.

In the general case, knowledge of all angles of vision is sufficient to determine the position of an object in space; for this, one should take one eight-dimensional excitation vector rather than four two-dimensional vectors. The direction of this vector determines unambiguously the location of the object in space. As shown by studies, the depth sensitivity of such a model would be lowest along the cyclopian axis. At the same time, in man sensitivity to change in distance of an object is maximal on this axis.

It is easy to eliminate this flaw. For this, let us plot a separate depth analyzer. It is assumed that it consists of a set of local analyzers. Each such analyzer examines only part of the visual space. Let us call the retinal regions on which the sector of space examined by a given local analyzer is projected the monocular receptive fields of the local depth analyzer. Each analyzer determines the "depth" of an object in relation to a point that is at the same distance as the fixation point (Figure 69). Let us call the geometric place of points in the horizontal plane and at the same distance as the fixation point the horopter. Thus, each local analyzer of depth measures the distance of an object in relation to the corresponding horopter point. This means that angles of vision are measured in each local analyzer in relation to the corresponding horopter point.

Disparity (Figure 69), in the form of difference in levels of excitation of monocular primary detectors with sinusoid sensitivity characteristics (Δ is the signal of horizontal disparity), is the input signal for primary detectors of the local depth analyzer. The level of excitation of gradual primary detectors of disparity in a given segment of space determines the components of the disparity vector, the direction of which is what gives the subjective sensation of position of an object in depth, its distance.

Output detectors can be formed by the usual method (Appendix 1). The structure of the depth analyzer is illustrated in Figure 69.

There is a set of pairs of local analyzers of direction of object. Each such analyzer has its own reference point, and two such points, *2* and *1*, are shown in the figure. Point *2* is on the cyclopian axis and with fixation thereof there is projection in points *2'* and *2'* on both retinas. Arbitrary point *4* is seen by both local analyzers simultaneously at angles of $\alpha_i + \alpha$, $\beta_i + \beta$ and α, β.

The presence of point *4* in the visual field of both analyzers elicits excitation of monocular primary detectors of direction of different eyes. The characteristics of these pairs of detectors are outlined with dashes. Then the signals from the local direction analyzers which distinguish in each eye the same direction interact and form a signal that is proportional to the disparity of the object in the visual field of the local depth analyzer in the specified direction:

$$\Delta_0 = \sin\alpha - \sin\beta \approx \alpha - \beta,$$
$$\Delta_i = \sin(\alpha_i + \alpha) - \sin(\beta_i + \beta) \approx (\alpha_i - \beta_i) + (\alpha - \beta).$$

If $\alpha_i - \beta_i = 0$, disparity of the object is the same in all analyzers. The bottom row shows two pairs of primary depth detectors with responses in the form of cos and sin $\lambda\Delta$. Each pair of these detectors is used to code the depth of an object in corresponding directions. Each excitation vector formed by primary depth detectors implements, through the fan of communication vectors, selective excitation of a secondary detector (this is not shown in the figure). We shall now discuss only one of the local depth analyzers. The monocular analyzers of "direction of object" are discussed only to the extent that they are necessary to describe the function of the depth analyzer, which codes depth over a considerably broader range of disparities than the rnage in which image fusion (Panum's area) is possible. Within Panum's area, along with the depth analyzer, there is function of the mechanism of image fusion; beyond the fusion area there is only one functioning depth analyzer, and this explains depth perception with diplopia.

However, the area of space examined by a local depth analyzer is limited. This area is determined by the receptive fields of the depth analyzer.

The conclusions derived by Beverley and Regan [94, 95], based on experimental facts, to the effect that there are at least four primary detectors of the analyzer of motion in depth serve as indirect confirmation of the fact that the depth analyzer is not an exception from the general rule of constructing analyzers.

Properties of model of depth analyzer. Horopter: The horopter is defined as the geometric site of points in three-dimensional space that have the same subjective direction with a given fixation point for the left and right eye separately.

Unfortunately, there is no agreement as to how a horopter is to be demonstrated experimentally. There are several methods of determining it [83, 84]. In one instance, the horopter is defined as the aggregate of points the angle of vision of which does not change when viewed alternately with either the left or right eye, with a specified fixation point. Thus, the horopter demonstrated in the horizontal plane coincides well with the so-called Fit-Muller circumference, i.e., the circle traced through fixation point Φ and the optical centers of both eyes. Angles α and β, at which any horopter point is visible to the left and right eye, respectively, are equal to one another. This is attributable to the fact that the apex of these angles rests on the same circle, while their sides rest on the same arc of this circle.

In the model of the depth analyzer, the monocular "direct of object" is determined by the direction of corresponding excitation vectors. For these directions to be equal for the left and right eye, the vectors must be collinear or, which is the same thing, angles α and β determining the values of vector components with low vertical disparity must be the same. Thus, the horopter is also a Fit-Muller circle.

Another method of experimental determination of a horopter is based on finding the geometric site of points in the horizontal plane, which are subjectively perceived as lying in the same frontal plane, with a specified fixation point. It is believed that the fixation point is also in this frontal plane. Thus, the frontal plane is a plane, each point of which has zero depth in relation to the fixation point. With this experimental definition of a horopter, utterly different results are obtained than by the method of same directions [83]. At small distances of the fixation point, the horopter coincides rather well with the Fit-Muller circle. As the distance from the fixation point of the subject increases, the slope of the horopter diminishes, coming close to a straight line. At a certain distance from the subject, the slope changes in sign, as a result of which the horopter becomes convex [83, 84]. In order to use this method for determination of the horopter of the model we must clarify what the term, "has the same depth as the fixation point," means. There can be two cases: 1) the distance in depth to arbitrary point A of the horopter is measured directly from the fixation point, and it is indicated that this distance equals zero; 2) the distance from this point is measured from a certain arbitrary point, the subjective reference point (in this case, the term, "has the same depth as the fixation point," means that arbitrary point A is just as far in depth from the reference point as the fixation point).

Unfortunately, there are no works dealing with the question of how the subject solves the problem put to him.

If we adhere to the first method of measuring distance for determination of the horopter in the model, the horopter line again coincides with the circle of Fit-Muller. The shape of the horopter will be different in the second case. Let us discuss this case in greater detail.

Let there be a certain point B on the cyclopian axis, which is selected as the subjective reference point. Let us define the distance in depth from point Φ to point B. It is determined by the direction of vector Д(Φ/B). The expression Φ/B means that the disparity analyzer measures the distance of point Φ in relation to point B.

With the second method of determination, the horopter is a surface in space, each point of which is at a same distance in depth from point B as point Φ. In other words, each point A of such a surface corresponds to a disparity vector D (A/B), which is collinear with vector D(Φ/B).

The results of calculation depend on determination of point B, the subjective reference point. Two cases are considered. In the first case, the position of the reference point on the cyclopian axis is fixed (Figure 70a) and in the second, the point of the subjective center follows the fixation point at the same subjective distance (1° or 30') (Figure 70, b, c) (Appendix 6).

With the second method of determination, the shape of the horopter differs from the horopter calculated by the method of equal directions. The slope of the horopter diminishes constantly as the fixation point moves farther away along the cyclopian axis. With sufficient distance of the fixation point, the slope of the horopter changes in sign, and it becomes convex. If, however, fixation point Φ coincides with reference point B, the horopter, as was to be expected, coincides with the circle of Fit-Muller. In both cases, the model is capable of explaining the shape of the horopter.

Mixture effects in the binocular analyzer: The proposed model has a limited number of primary detectors at its input. Each specific set of stimuli of these detectors determines the number of output element with maximum excitation. However, primary detectors can be excited to the same level by different means, by different combinations of stimuli. Excitation generated by one stimulus may be indistinguishable from excitation generated by several stimuli delivered simultaneously. As a result, the model will be incapable of differentiation between one stimulus and the overall effect of two stimuli. This phenomenon is known as the depth mixture phenomenon [16].

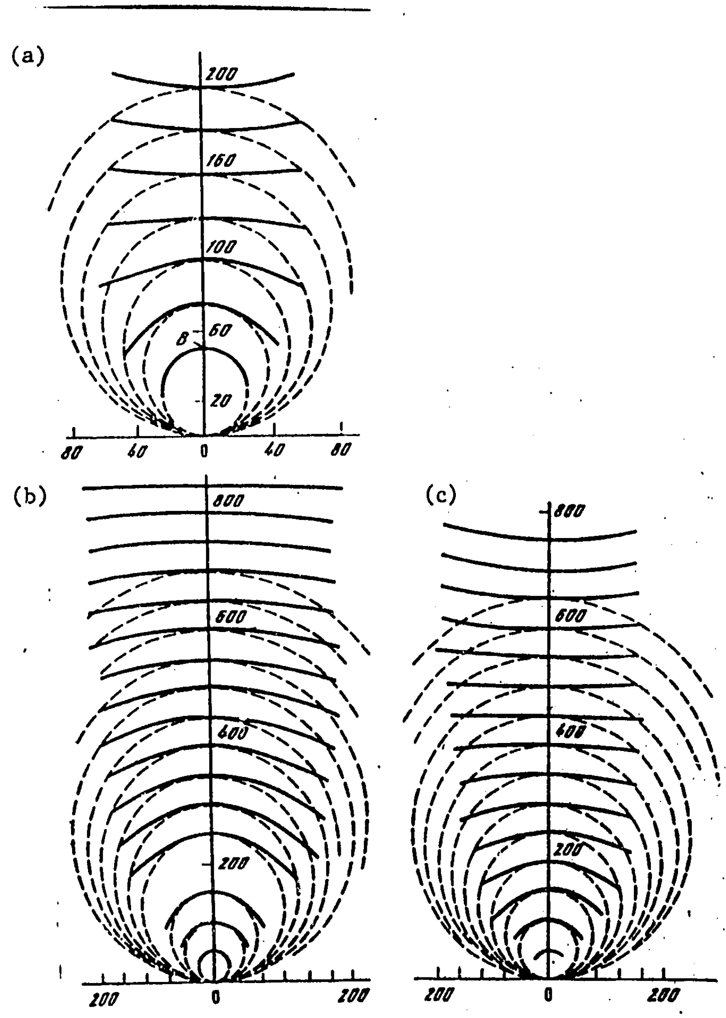

Figure 70. Horopter as the geometric site of points that are equidistant in depth in relation to fixation point B. X-axis, distance from cyclopian axis; y-axis, distance in depth along cyclopian axis

a) reference point is fixed and located on the cyclopian axis at point B (OB = 50 cm)

b,c) reference point follows fixation point and is situated on the cyclopian axis at an angle of vision of 30', 1°

Let us consider in greater detail one of the described experiments which, in the authors' opinion, is indicative of existence of the depth mixture phenomenon in the binocular analyzer [16]. Figure 71 illustrates the stimuli used in the experiments of Foley. An illuminated fixation point Φ was presented on a screen to the subject, and below it were two lines, L_A and L_B. The position of the lines was such that the image of line L_A on the left retina and of line L_B on the right one had zero disparity, i.e., the angle of vision of line L_A with the left eye equaled the angle of vision of line L_B with the right eye, while the angle of vision of L_B with the left eye equaled the angle of vision of line L_A with the right eye.

As a result of such matching of stimuli there was fusion of two images objectively referable to different lines.

During the experiment, the intensity of luminescence of L_A (or L_B) was constant, whereas the experimenter could alter it for $L_B(L_A)$ at will.

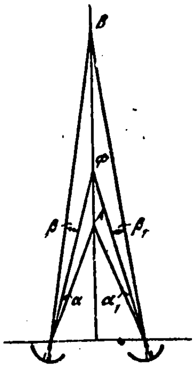

Figure 71.
Depth mixture according to Foley [16] (Lines L_A and L_B are at points A and B, and the perceived depth equals the sum of their depths)

By means of special devices, the subject was able to indicate the perceived depth of lines L_A and L_B in relation to the fixation point. If the intensity of luminescence of lines L_A and L_B was the same, the subject perceived them as being at the same depth as the fixation point. With decrease in intensity of either line, L_A (or L_B), there was a change in perceived depth of the resultant image, approximating the more illuminated line, L_B (or L_A).

Thus, there is "mixture" of depths of the lines when viewing two lines that are objectively at different distances from the fixation point. As a result of such mixture, the subject perceives one line at a certain intermediate depth. The brighter the relative brightness of each line, the greater its "contribution to perception of resultant depth.

There is a simple explanation for the mixture effect in the model. Each of the lines excites separately the same primary detector whose output signal is the sum of effects of both lines. The degree of detector excitation depends not only on disparity of the image on the retina, but intensity of each of them. By altering the intensity of luminescence of the stimulus we alter the contribution of this stimulus to excitation of primary detectors.

As a result, there is depth mixture of two stimuli, and the brighter the stimulus, the greater its contribution (Appendix 6).

Simultaneous contrast and adaptive effects in object position analyzer: To increase discrimination of two successively delivered stimuli, let us add into the depth analyzer an adaptation mechanism for attenuating sensitivity of primary detectors as a function of excitation level they have reached. The illusion of adaptation is the "price" for this gain: aftereffect and normalization effect. The aftereffect consists of the fact that prolonged viewing of distant points leads to seeming approximation of the initial fixation point, whereas viewing close points leads to increase in distance of the fixation point. Adaptation in the depth analyzer will also generate the normalization effect--seeming change in depth of object in the form of its approximation to the fixation point.

There have been previous reports [96, 97] of the effect of prior adaptation on subsequent estimation of depth of a test object. A more recent study of the aftereffect phenomenon in human depth perception was conducted by Mitchell et al. [98]. The main conclusion of this study was that the distance to a test object was overestimated after adaptation to a nearer stimulus. After adaptation to stimulus that was farther away than the fixation point, the subject presented a tendency toward underestimating the distance to the test object. Thus, the aftereffect observed in the experiments had the same features as in the model.

Lateral inhibition, the consequence of which is depth contrast [99], is introduced between homonymous primary detectors of local analyzers of disparity in order to improve the model's discrimination of two objects presented simultaneously at different depths.

Anomalies of depth perception: The primary detectors of the depth analyzer differ from the primary detectors of the monocular analyzer of "direction of object," whose properties are similar to those of detector neurons of angular dimensions [93]. The difference is that signals are delivered to disparity detectors from monocular detectors referable to different retinas. The detectors of one retina have an excitatory effect on depth detectors, while the detectors of the other retina have an inhibitory effect. Let us consider a detector for which the left eye is a source of excitation and the right a source of inhibition. If we consider that a real neuron cannot transmit a negative signal, there must be neurons whose responses are expressed separately as the positive and negative parts of the responses of a "theoretical" primary detector (Appendix 6). The wider the angle of vision of an object with a given eye, the stronger the signal from monocular detectors with sinusoidal responses. Consequently, the primary detector, for which the left eye is excitatory, will react only to objects for which the angle of vision with the left eye is larger than the angle of vision with the right eye, i.e., this primary detector is excited only if the object is farther away than the fixation point (Appendix 6). Analogously, the neuron with excitatory input from the right eye will react only to objects situated closer than the fixation point (however, together they realize the response of the theoretical detector).

If one of these detectors is missing from the depth analyzer, the entire system will be incapable of perceiving either greater distances, or distances that are closer than the fixation point. Such disturbances of depth perception have been described in the literature [97, 100].

Absence from the visual system of one of the above-described primary detectors of disparity does not mean that the subject will be unable to determine whether a given point is closer or farther than the specified fixation point. Let there be no detector of close objects in the visual system, as a result of which the subject cannot determine that point A is closer than fixation point Φ. The subject will settle the question of depth of objects in the following manner. The subject will replace fixation point Φ with point A and determine that former fixation point is farther away than point A, i.e., point A is closer than point Φ. In other words, the subject solves the problem of depth using the analyzer for objects that are farther than the fixation point, since he does not have a directly available analyzer for objects that are closer than the fixation point.

It has been experimentally demonstrated that the behavior of a subject with anomalous binocular vision when solving "closer--farther" problems is very similar to the above-described behavior of the model in solving analogous problems [100].

Thus, it can be maintained that the experimental facts are consistent with the assumption that the human and animal depth analyzer has the structure of a standard analyzer, which codes signal parameters by channel number.

Construction of eye position analyzer. When discussing the question of constructing an analyzer of line of vision, one must take into consideration that the line of vision of each eye is determined by two independent variables: position of the line of vision in the horizontal plane and position of the line of vision in the vertical plane. This situation is analogous to coding an object in space in relation to the fixation point. The difference is that, in the case of coding eye position, there is localization of fixation points, whereas the depth analyzer codes the position of an arbitrary point in relation to the fixation point. Thus, the task of constructing an analyzer of direction of line of vision can be solved by analogy with the stereo analyzer. The degree of tension of corresponding eye muscles serves as the input signal of primary detectors. The gauge for angle of rotation of the photomatrix (eye) in the horizontal (or vertical) plane generates a signal that equals the cosine and sine of this angle of rotation. These signals are formed at the output of two primary detectors. They are followed by a second layer of selective detectors connected to primary detectors by connections that differ in weight coefficients. With change in the angle characterizing the orientation of photomatrices in relation to external space, an excitation maximum is created on one of the detectors that codes this position of the photomatrices. Each fixed position of the line of vision of the photomatrix corresponds to maximum excitation of a specific detector. When the eyes turn, the degree of excitation in primary detectors changes and the excitation maximum shifts along the set of detectors of position of line of vision. The distinction of this structure is that, at each point in time, there is only one excitation maximum on the chain of detectors that determines the only position of the line of vision at each point in time. There is a quasireceptive space of detectors of position of line of vision for the entire space, in which the line of vision may have a different position. With any change in direction of vision in depth or angle, in relation to the horizontal plane, there is a shift of excitation maximum in it, reflecting the shift of the line of vision.

The line of vision in depth, in relation to the horizontal plane, does not alter the viewed position of a target, although its position on each retina and on the stereo detectors changes. We have to assume that, at a higher level, signals of eye position are considered in some way, providing for constant perception of the objectively stable world. To solve this problem, let us use the mechanism of invariant detectors that we have already discussed. It consists of the fact that the detectors of direction of vision alter the communication vector of the cyclopian screen with invariant detectors uniquely, so that with concurrent change in position of signals on the cyclopian screen and detectors of position of line of vision of the stereoscopic picture of the outside world on the set of invariant detectors does not change. Stereo signals are read in relation to the initial fixation point. It should be noted that with change in fixation point the disparity of image on the left and right retina may exceed the permissible range, i.e., the object will move beyond Panum's area. As a result, there could be destruction of perception of a fused image, diplopia may arise. However, this will not happen if we take into consideration the hysteresis effect in the stereo analyzer. It consists of the following: after fusion of an image has occurred (superposition of images on the left and right retina to form one stereoscopic image), it will be destroyed only when disparity exceeds significantly the range defined by Panum's area [89]. Evidently, this effect is implemented by lateral connections between sets of detectors on which the fused image appears. As a result, moderate wandering of the line of vision will not disrupt the fused image, while the presence of invariant detectors will provide for invariant perception of the outside world.

The mechanism of construction of invariant detectors is consistent with the general scheme described before.

Each detector of the aconstant stereoscopic screen is connected to all invariant detectors. However, the connections between aconstant and invariant detectors can be selectively altered, depending on localization of excitation maximum on the population of detectors of position of line of vision. For example, let the orientation of matrices be such that there is maximum excitation of the kth detector of position of line of vision. This is associated with activation of connections between the first aconstant and kth invariant detectors, second and $(k+1)$th detectors. As a result, distribution of excitation on the set of invariant detectors is shifted by k units in relation to the distribution on the set of aconstant detectors. If orientation of the photomatrices changes, there is concurrent change in position of the image on them. A shift of the image on the matrix leads to shift of excitation maximum on the set of detectors of position of line of vision. It is assumed that the shift in maximum on detectors of position of line of vision would lead to a change in connections between aconstant and invariant detectors, with which the distribution of excitation on invariant detectors will be shifted by the same number of units to the left of the distribution of excitation on the set of aconstant detectors. Thus, the excitation maximum on the invariant set of detectors will again be found on the same kth detector. Thus, a shift of images caused by movement of matrices (eyes) on the set of invariant detectors will be automatically compensated by a shift of line of vision.

Since the detectors of position of line of vision change only the destination of visual signals on the invariant screen, rather than excitation in the visual channel, the visual image itself does not change.

A robot with an invariant screen of reflection of the external environment will have the same illusions as are inherent in human vision. Thus, if the distribution of light on photomatrices remain constant, while the matrices turn in such a manner that signals will arise in the turn sensors corresponding to a shift of the robot's line of vision, there will be a shift of signals on the invariant screen. This will be perceived as a shift of the stimulus in space. An analogous situation arises in man's perception of an afterimage. For example, prolonged viewing of a white square on a black background leads to appearance in the dark of an after image after the former is turned off: black square on a white background. Movement of the eyes leads to the sensation of movement of the afterimage, although there is actually no shift of the illusory image.

The entire diversity of aconstant detectors reflects the external space with all possible combinations of image shifting in relation to the photomatrices. The space of the invariant detectors involves all of the objective space that can be represented on invariant detectors by altering the position of the line of vision.

With addition of short-term memory into the mechanism of operation of invariant detectors we have the possibility of constructing a panoramic image of the external world on the invariant screen, even if the size of the aconstant screen is limited.

CHAPTER 8. GRAVITY ANALYZER

Neuronal mechanisms of perception of gravity. The gravity analyzer is represented by otolith organs in vertebrates--the sacculus and utriculus. The most important elements of these organs are receptors invested with cilia--kinocilia and stereocilia, thanks to which the receptors are sensitive to the direction of force of gravity. If an exogenous force leads to deflection of kinocilia away from the stereocilia, depolarization occurs in the receptor. If gravity acts in the opposite direction, toward the stereocilia, hyperpolarization occurs in the receptor. The otolith receptors form a group of several hundred units, in each of which the kinocilia are oriented in the same direction. However, the orientation of kinocilia in different groups is not the same. This causes each group of receptors to be a selective receiver of specific directions of gravity. On the surface of the macula formed by hair cells the lines of polarization of kinocilia diverge from the medial region to the periphery, where the direction of polarization is reversed. With a change in gravity, there is selective excitation of the group of hair cells where the direction of the gravity vector coincides with the orientation of kinocilia. Thus, the receptors of the sacculus and utriculus are receptors of direction of gravity. The utriculus differentiates finely a deviation from the strict vertical position, while the sacculus differentiates all other positions. Detection of the direction of gravity is made with the participation of otoliths, which are fine grains of calcite. Tangential displacement of cilia, which could reach 15 μm with extreme inclination of the body, is the stimulating factor. The receptors are synaptically connected with neurons of Scarpa's ganglion. The ganglion neurons present selectivity for the direction of the gravity vector. Ultimately, the otolith signals can be used to control body movement in order to maintain equilibrium: different parts of the macula or, more precisely, different groups of its receptors with specific polarization are connected to different muscle groups.

Differentiation of the gravity analyzer into two regions with groups of selectively oriented receptors in different areas makes it difficult to give a formal description of the gravity analyzer. It is considerably simpler to introduce formalism to describe the vertebrate organ of equilibrium.

Statocysts of mollusks. The mollusk statocysts are sacs, 70-100 μm in diameter, which are symmetrically situated between pedal and cerebral ganglia. The statocyst is transparent, and it consists of 12-13 hair cells 40-50 μm in diameter. The cilia of hair cells, totaling 100-150, are oriented into the statocyst. There is an accumulation of particles, 3-10 μm in diameter, which are called statoconia, in the fluid inside the statocyst. An inclination of a statocyst causes shifting of the accumulation of particles in it in the direction of inclination. Some cilia bend. With delivery of a mechanical pulse from a piezocrystal to a statocyst, the hair cells forming its walls move, while the cilia bend under the influence of particles with inertia. The generator potential of hair cells increases linearly as a function of the logarithm of statocyst displacement. The hair cells form axons, along which impulses generated by them travel to the centers of the cerebropleural ganglion.

If an isolated statocyst is rotated, the centrifugal force which occurs during rotation causes statoconia to compress cells located farther from the center of rotation, their cilia bend over, the cells are depolarized and impulsation frequency increases. Centrifugal force attenuates the effect of statoconia on the cilia that are closer to the center of rotation. Their cilia stand erect, the cells are hyperpolarized and impulsation frequency in them diminishes. Threshold stimulation of hair cells constitutes 0.5-0.25 G. There is inhibitory interaction between hair cells, which increases the difference between reactions of hair cells situated in different parts of the statocyst. Thus, the entire population of hair cells forms a receptive surface in the form of a closed sphere. The receptors perform a detection function. Gravity elicits an excitation profile on the receptors. The excitation maximum is localized in a specific part of this receptive surface, depending on the body's position in space.

With change in body position, the gravity vector changes in relation to the set of receptors and excitation maximum shifts over the sphere formed by the cilia. Here, the direction of gravity is coded by channel number already on the level of the receptors that transmit signals directly to nerve centers. Thus, although there is no multilayer detector system in the analyzer of direction of gravity, the receptors perform the function of coding by channel number. The spherical structure represented in the above-described cases in the form of a quasireceptive surface formed by detectors is realized here by the receptive surface itself. Since there are no primary detectors here, illusions related to adaptation on the level of primary detectors are also not observed. Lateral inhibition, which occurs between hair cells, increases selectivity in coding of the gravity vector by channel number.

Gravity analyzer with neuron-like elements. One can construct a statocyst technically in the form of a closed sphere, within which there is a weight attached to guys. These guys are situated at a fixed distance from one another on the sphere, and they are equipped with pressure sensors.

Let us bisect the center of the statocyst in the plane of gravity. Then the weight would be suspended on the guys and lean on supports situated on the circumference. If we assign numbers to the guy-supports, the gravity vector will create pressure that differs in magnitude and sign in guys having different numbers. The signals taken from the corresponding pressure sensors form the pressure profile. With a change in direction of the gravity vector, the pressures are redistributed on the guys, creating a new pressure profile. The pressure in each of the guys determines the magnitude of components of the excitation vector. Then the differences between directions of gravity vectors will be determined by the angle between the excitation vectors they create. If we were to describe the components of the excitation vector as polar coordinates, there is a specific orientation pattern in three-dimensional space corresponding to a specific direction of gravity. With change in direction of gravity, the orientation pattern shifts over the sphere formed by receptors.

Addition of reciprocal inhibitory connections between receptors makes it possible to code the direction of gravity more selectively by channel number.

Screen that is invariant in relation to gravity vector. When the position of the robot's housing changes in space, there is a shift in signal image on the photomatrix. This image shift can be eliminated by introducing an invariant screen, with projection on which of an exogenous stimulus there is consideration of the position of the robot's housing in relation to the gravity vector. In constructing the invariant screen, the main element is an invariant detector whose communication vector with corresponding detectors of the aconstant screen are readjusted under the influence of signals from the auxiliary set of detectors. A population of gravity detectors can serve as such an additional set of detectors. The excitation vector of the gravity detectors performs the same function as the excitation vector formed by the detectors of eye position. The excitation vector formed in the guy-support sensors alters the coefficients of communication of detectors of the aconstant screen with detectors of the invariant screen in such a way that the image remains on the same elements with all changes in position of photomatrices in relation to external space when the robot bends over.

CHAPTER 9. CONSTRUCTION OF ANALYZERS TO ORDER

Requirement of analyzer constructed of neuron-like elements. We have discussed above general theory of artificial sense organs based on the principle of coding signals by channel number. Then this theory was tested on models of specific sensory systems. The properties of the sensory system constructed with neuron-like elements were compared to the psychophysical and neurophysiological features of the corresponding real analyzers. The constructed models, which reproduced the functions of real sense organs on the psychophysical level, had a remarkable property: the responses of their neuron-like elements coincided with the responses of real neurons.

Thus, the principle of coding by channel number turned out to be effective in modeling specific sense organs. The fact that the psychophysical and neurophysiological features of the models and real biological analyzers coincide opens up the possibility of designing new artificial sensory systems that man does not have on the basis of the principle of coding by channel number.

Let us discuss the process of constructing an artificial sensory system, an analyzer of polarized light. By selecting this analyzer as an example of sensory system that man does not have, we can check the effectiveness of modeling on biological objects, since insects have such analyzers.

We now come to the problem of constructing a robot analyzer that distinguishes a light source according to plane and degree of polarization.

Detection of polarization plane must be independent of the angle of inclination of the robot. For this reason, at the final stage one must provide for constant perception of polarization plane by taking into consideration information taken from detectors of the robot's position in space.

Detectors that are selective to plane and degree of polarization. Let us consider detectors that code the position of the polarization plane in relation to the horizontal plane. The polarization plane is characterized by an angle that can have any value in the range of 0-180°.

We must have at least two independent primary detectors to code the angle of polarization. The level of excitation of each primary detectors determines the value of components of the excitation vector. In view of the fact that negative signals require a special channel, there must be four primary detectors. The direction of the excitation vector codes the angle of polarization. Signals from the four primary detectors, whose responses are so chosen as to have a constant modulus of the excitation vector, are fed to the inputs of secondary detectors. In this case, the ends of the excitation vectors remain on the sphere, in this case on the circumference. The increase in number of primary detectors to four provides for transmission of the signal even when it has a negative value.

When the designed model must provide coding not only of polarization angle, but degree, the minimum number of primary detectors required increases to three or five, respectively.

The responses of primary detectors of polarized light can be represented by a sine or cosine of a dual angle of polarization, analogously to what occurs in the primary detectors of line tilt.

Ordinary photoresistors covered with film, with polarization axes of 0 and 45°, can serve as receptors of polarized light. In an analyzer that considers not only the angle but degree of polarization, one can use a receptor without selectivity for polarized light to construct the auxiliary primary detector.

The characteristics of receptors [101] that are selective for polarization plane do not provide directly for optimum responses of primary detectors, since they contain a constant component. In order to obtain responses of primary detectors in the form of sine and cosine curves, one must subtract the constant component from the signal of the receptor that is sensitive to polarization plane.

The primary detector with a cosine curve type of response receives excitation from the receptor that is sensitive to polarization plane and inhibition from the receptor that is not selective for angle of polarization of light. As a result of such interaction, there is a signal in the form of a cosine curve at the output of the summating element. The summating elements constructed in this way can be used as primary detectors.

Two more additional primary detectors, on which an unpolarized receptor has an excitatory effect and receptors sensitive to angle of polarization of light have an inhibitory effect, must be constructed to transmit the positive and negative parts of the responses of primary detectors. These elements will have the responses that are necessary in transmission of information about the angles of polarization, with which the value of the corresponding cosines is negative (Figure 72). Two receptors have selectivity for the polarization plane. One receptor is not sensitive to the polarization plane. The optimum angles of orientation of receivers of polarized light are 0 and 45°. The primary detectors are formed by paired summation of a selective and nonselective receptor with different signs. The signals of primary detectors form a three-component excitation vector. Secondary detectors lie on the sphere.

The analyzer that codes the degree and angle of polarization of light is analogous to the color analyzer. Like color, polarized light is characterized by two parameters--degree of polarization and angle of polarization (the degree of polarization is analogous to saturation in the color analyzer, while the polarization plane is analogous to color tone). When reflecting an exogenous signal on the sphere, the vertical angle on the sphere characterizes the degree of polarization of light, while the horizontal one characterizes the inclination of the polarization plane (Figure 73). If the degree of polarization changes and the angle of polarization remains constant, the point on the sphere moves along the meridian. If, however, only the polarization angle changes, the point on the sphere representing the

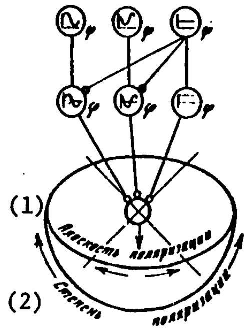

Figure 72.
Structure of analyzer of plane and degree of polarization of light
1) polarization plane
2) degree of polarization

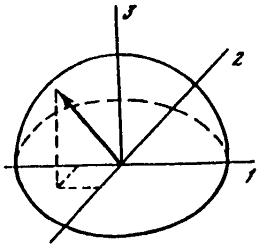

Figure 73.
Spherical model of analyzer of plane and degree of light polarization
1, 2) selective detector adjusted for 0 and 45°, respectively
3) nonselective primary detector

stimulus shifts along the parallels. The three-component excitation vector executed by means of three primary detectors determines through the set of connections the location of the secondary detector with maximum excitation, each such detector being localized on the sphere. With change in degree of polarization there is change in relative contribution of the nonselective primary detector. This leads to change in excitation maximum on the sphere. There is a detector of unpolarized light on the pole, which is an analogue of the white detector in the color analyzer. With change in polarization plane there is change in position of the excitation maximum, which is characterized by the horizontal angle, the analogue of color tone in the color analyzer. Thus, the analyzer of plane and degree of polarization is an analogue of the color analyzer. The color white corresponds to unpolarized light, while a change in color tone corresponds to change in plane of polarization.

Polarized light analyzer. There are three receptors at the input of the biological analyzer of polarized light in insects. One of them is not selectively sensitive to polarized light. The other two have maximum sensitivity to different angles of polarization. For these receptors, the angle between optimum axes of polarization of light equals 45°. The sensitivity of the receptor to polarization angle is determined by orientation of rhodopsin molecules in the microtubules of the reticular cell rhabdomere. Usually, the polarization axes of photoreceptors are so oriented that with a 0° angle of polarization of light both primary detectors are equally exicted [101]. This means that, in this case, all of the components of the excitation vector are equal. Such a vector does not change its direction with adaptation. Thus, the model is similar to a real biological analyzer.

To distinguish light according to degree of polarization, use is made of a receptor of unpolarized light whose rhabdomere is twisted in relation to the longitudinal axis in such a way that it reacts the same with all polarization angles. The higher levels of the biological analyzer have not yet been studied. In the model, the secondary detectors are constructed by the usual method: a communication vector that is collinear to the excitation vector whose direction codes this secondary detector is assigned to each detector.

With change in plane or degree of light polarization, the excitation maximum shifts from one primary detector to another. This corresponds to displacement of the point representing the stimulus on the sphere. The position of this point on the sphere is characterized by two angles: vertical angle that determines degree of polarization and horizontal angle that determines the angle of polarization of light. We could continue the analogy to the color analyzer. To the four opponent neurons of the color analyzer correspond four primary detectors in the polarized light analyzer. The analogue of the black and white system is the primary detector of degree of polarization. Secondary detectors of degree and angle of polarization correspond to the selective color detectors.

The polarized light analyzer also has a normalization effect. Polarization angles of 0, 45, 90 and 135° are stable, while 22°30', 67°30', 112°30' and 157°30' are unstable. In addition to normalization, there is also an aftereffect. During prolonged viewing of polarized light, the sensitivity of each primary detector changes as a function of degree of its excitation. For this reason, the next stimulus could excite primary detectors in a different proportion, as compared to what would happen without adaptive stimulus. The adaptation effect leads to the illusion of change in polarization plane.

Constant perception of polarization plane by using gravity analyzer signals. In the model discussed, a specific angle and degree of polarization correspond to a selective secondary detector, in which the only excitation maximum occurs. If the angle or degree of polarization is changed, excitation maximum shifts from one detector to another. Thus, in this system signal coding is done by channel number. However, such a set of detectors is not constant, in the sense that with a constant angle and degree of polarization inclination of the equipment containing the polarized light analyzer also leads to a shift of excitation from one detector to another. It can be said that many [or a set] of detectors of polarized light form a quasireceptive surface of the aconstant type. In order to render perception of polarization angle constant--independent of inclination of apparatus--we must create a quasireceptive surface of invariant detectors. Each invariant detector is connected to all aconstant detector; however, the link between aconstant and constant detectors changes in accordance with the excitation vector on the set of detectors of the analyzer of direction of gravity.

When the apparatus is inclined, the plane of polarization of light changes in relation to the photoreceptors; concurrently, there is change in direction of the excitation vector in the gravity analyzer which, in turn, leads to change in communication vector between the sets of invariant and aconstant detectors. As a result, when there is concurrent change in polarization plane and angle of inclination of the apparatus, excitation maximum remains on the same invariant detector. At the same time, if only the polarization plane changes, excitation maximum shifts from detector to detector, reflecting the change in the external world on the quasireceptive surface of invariant detectors. The cost of constancy of perception is the illusion of seeming change in polarization plane when the signal of the gravity analyzer is not accompanied by a change in polarization plane.

Control of apparatus [robot?] movement by means of command elements. The significance of a constant screen formed by invariant detectors of polarization plane is graphically demonstrable when it is necessary to control an apparatus moving toward a target that is determined by a given plane of polarized light. Indeed, with any inclination of the apparatus the excitation maximum remains on the same invariant detector in accordance with the objective constancy of the plane of light polarization. Let us consider the case when the apparatus must move toward a light source characterized by a specific angle of plane of light polarization. The apparatus has two modes: search for target and movement toward target. If the signal on the set of detectors coincides with the set one, the apparatus operates in the mode of movement toward the target. If the angle of polarization of light falling on receptors differs from the specified one, the apparatus operates in the mode of searching for the target by means of circular scanning [survey]. One can set the mode of operation by using command elements. One command element turns on the program for movement toward a target, The second command element turns on the scanning program. There are inhibitory connections between the command elements. To switch from one mode to another, the invariant detector representing the target is conncted to the command element for the mode of movement toward the target. All other detectors are connected to the command neuron for searching for the target. If a light source with specified polarization plane appears in the field of vision, the program for moving toward the target is turned on and the scanning one is turned off. If radiation falls on receptors that has a different angle of polarization plane, the program for moving toward the target is turned off and the search program is turned on. If, in the course of scanning, the apparatus assumes a position, in which the polarization angle coincides with the required position, the excitation maximum occurs on the invariant detector connected to the command element for movement toward the target. As a result, the scanning program is turned off and the program for moving toward the target is turned on. Since invariant detectors are used, movement of the apparatus toward the target is not impaired by any inclination of the apparatus where the plane of light polarization in relation to receptors changes.

The appropriate invariant detector is connected to the corresponding command element in order to control the choice of targets. Thus, the question of resetting [readjusting] the apparatus amounts to changing the connections of the command neuron to a specific detector. In order to change the target, one has to disconnect the previously connected detector from the command element of movement toward the target and connect another detector to it. This changes the target toward which the apparatus moves. Moreover, the disconnected detector must be connected to the command element for scanning. Such complex alteration of connections can be made by means of controlling the coefficients of communication of detectors with command neurons. For this purpose, one uses a modifying vector which goes to the set of connections in the form of two mutually complementary copies: one copy alters the connections of detectors with the command neuron for movement toward the target and the other with the command neuron for scanning. As a result, there is concurrent disconnection of detectors from one command neuron and connection thereof to another command neuron. After this, movement toward the target is triggered by another detector. The detector which previously turned on the program for movement toward the target then becomes one of the detectors that turns on the scanning program.

Thus, by comparing the coding of external signals in the central nervous system to the pattern of neuronal discharges, ensemble of neurons and channel number, it can be concluded that coding is done by channel number by means of neuron-detectors that are selectively adjusted for specific values of the analyzed signal parameter. The distinction of coding by channel number is that the process of transmission of information is combined with processing thereof in parallel channels. The existence of a system of detectors acting in parallel provides for highly reliable coding. Elimination of part of the detectors does not disrupt appreciably the reflection of signals on the quasireceptive surface formed by the set of detectors. Presentation of the signal of excitation maximum on the quasi-receptive surface of the detectors is the logicalcontinuation of signal reflection on a receptive surface. However, the stimulus does not shift over the receptors in the case of a set of detectors. The stimulus merely alters the correlation between excitations of receptors. But maximum excitation does really shift over the set of central detectors. This shift of excitation maximum is achieved because each detector has its own set of communications with receptors.

The mechanism of constant perception is a more complex form of signal detection. In this case, the connections between detectors and receptors or primary detectors are not fixed. They change when the signal changes on the auxiliary set of detectors. When the organism itself moves, the signal changes both on the main and auxiliary sets of detectors. As a result, the excitation maximum remains on the same invariant detector. Invariant detectors make it possible to receive signals constantly, independently of the organism's movements. Construction of invariant detectors makes it possible to create the analogue of constant perception for a robot.

Representation of a signal in the form of maximum excitation on the quasireceptive surface of detectors makes it possible to use detectors and, first of all, invariant ones to control movements. This also applies to robots with artificial sense organs based on neuron-like elements. Signal coding with the channel number does not require recoding in the usual sense of the word in order to implement control functions. Signals from detectors can be used directly as control signals. Thus, coding by channel number provides for efficient transition from the alphabet of stimuli to the alphabet of reactions.

Coding by channel number is a universal method of coding in various sense organs based on common principles. The most common [general] principle is the principle of maximum sensitivity of a set of detectors. According to this principle, the detector characteristics should be so selected as to have maximum sensitivity of the entire set. On the basis of this principle, one can calculate theoretically the detector characteristics; these characteristics are found to be cosine curves. An external signal generating maximum excitation on one of the detectors can be represented by a point on an n-dimensional sphere.

One can accentuate detector responses by means of lateral inhibition, the magnitude of which is inversely proportional to the distance between detectors on the n-dimensional sphere. Here again, we see the analogy to simpler systems, for example, lateral inhibition in the Xiphosura eye.

The characteristics of receptors are coordinated with selective detectors by means of a layer of primary detectors that perform the function of a cosine.

Adaptation on the level of primary detectors renders the entire set of secondary detectors particularly sensitive to changes in a long-acting signal. In the case where there are several independent local analyzers, each of which has separate sets of primary and secondary detectors, lateral inhibition is added between homonymous primary detectors of local analyzers to enhance their differential sensitivity.

Lateral connections between homonymous primary detectors enhance discrimination sensitivity with regard to spatially scattered signals.

On the basis of the general scheme of organization of analyzers, one can create artifical sense organs for a robot that are based on neuron-like elements and reproduce the functions of real detectors. The artificial sense organs constructed on these principles are analogous in many respects to human and animal sense organs. Such an artificial analyzer as a whole reproduces the psychophysical characteristics that are known in man. At the same time, each neuron-like element corresponds to a real neuron involved in performing a given sensory function. As a result one can obtain an "internal" reflection of the environment in a robot that coincides with internal reflection of the environment in man. The similarity of perceptive characteristics of man and robot can extend to occurrence of analogous illusions. In both cases, illusions are the price for greater discriminating sensitivity. The resemblance of internal reflections in man and robot opens up new opportunities for efficient control of robots and creation of a reliable language to communicate with them.

Studies and formalization of general principles of neuronal organization of analyzers enable us not only to construct robot sense organs by analogy to the known human sense organs, but to develop on these principles sense organs in a robot that do not exist in man. In the most general form, construction of a set of detectors consists of having a specific input signal correspond to the number of a specific output detector.

The principle of coding by channel number in biological systems extends to organization of motion by means of command neurons. Channels formed by many [or a set of] detectors can be used directly to control robot movement. This is achieved by using command neuron signals in the structure of the robot.

Excitation of one analogue of a command neuron is transformed into a vector of excitations on a set of effector elements, which are motoneuron analogues. Thus, the channel formed by the command element at the output creates a specialized reaction. Here, the program of motion is fixed in the set of connections leading from the command neuron to the effector element. In order to use detectors for alternate control of reactions via command elements, the detector inputs on the command neuron must be flexible and depend on the number of deliveries of each signal, as well as which command neuron input is activated. Moreover, the communications between detectors and command neurons may change from an hierarchically higher level by means of signals that alter the sets of connections between detectors and command neurons. The reactions of the robot are functions of memory and instruction as a result of connecting detectors to command neurons and disconnecting detectors from command neurons, thus changing the correlation between stimuli and reactions.

Development of artificial sense organs based on the principle of signal coding by channel number also solves the problem of developing prostheses of lost sense organs by means of direct linkage of electronic devices to the neuronal structures of the human brain.

APPENDIX 1. GENERAL THEORY

Signal coding by channel number. Signal coding by channel number will be construed as coding where a specific value of a signal corresponds to one maximally excited element of a whole set. We shall call the different selectively excited elements detectors. A change in stimulus is transformed into a shift of excitation maximum from one element to another.

The set of detectors, together with elements that generate excitation under the influence of a stimulus, makes up the neuronal analyzer.

A detector that codes a certain parameter $\phi \in L$ of stimulus S_ϕ is viewed as an adder that summates paired products: occurring excitation by the coefficient of efficiency of synaptic contact c_{ji}:

$$d_j = \sum_{i=1}^{n} c_{ji} f_i = (\mathbf{C}_j, \mathbf{F}), \qquad j = 1, \ldots, m, \quad \varphi = \text{const},$$

where f_i are excitations over the ith input; the set of excitations $\{f_i\}$, $(i = 1, \ldots, n)$ is considered as components of excitation vector $F(\phi)$; c_{ji} is the coefficient of the ith connection of an underlying element with the jth detector; set $\{c_{ji}\}$, $(i = 1, \ldots, n)$ is considered as components of communication vector of the jth detector; d_j is the level of excitation of the jth detector. The input channels, which supply information to the detector, are linearly independent inputs. Thus, the number of inputs is finite, while functions $f_i(\phi)$, $(i = 1, \ldots, n)$, which describe sensitivity of the ith input as a function of ϕ, are linearly independent. Each stimulus S_ϕ generates excitation $\{f_i(\phi)\}$ at the detector inputs. Primary detectors may sometimes coincide with receptors. In other cases, primary detectors are the result of preprocessing of receptor signals:

$$S_\varphi \overset{\mathcal{B}_1}{\Rightarrow} \mathcal{R}(\varphi) \overset{\mathcal{B}_2}{\Rightarrow} \mathbf{F}(\varphi),$$

where $F(\phi)$ is the excitation vector; $\mathcal{B}_1$ and $\mathcal{B}_1$ are stages of conversion. $\mathcal{B}_1$ implements the transition from stimulation to the receptor excitation set, while $\mathcal{B}_2$ does so from the set of receptor excitations to the set of excitations of primary detectors.

The level of excitation of the jth detector under the influence of fixed stimulus S_p is determined with the following equation:

$$d_j=(\mathbf{F}_p,\ \mathbf{C}_j)=|\mathbf{F}_p||\mathbf{C}_j|\cos[\mathbf{F}_p,\ \mathbf{C}_j].$$

The problem of constructing the analyzer for signal coding by channel number amounts to finding for each secondary detector the communication vectors C_j that would cause this detector to be maximally excited from a given stimulus, in relation to all other detectors in the set.

We see from the equation for d_j that if contacts C_j are matched and fixed the position of the maximum on the set of detectors is unrelated to the value of vector modulus $|F_p|$. This means that coding with channel number is equivalent to coding the signal parameter with the direction of the excitation vector.

The simplest solution to the previously formulated problem is obtained in the case where $|C_j|$ = const. It is obvious from the equation $d_j = |C_j||F_p|\cos[C_j, F_p]$ that achievement of maximum excitation of the jth detector with a fixed stimulus S_p is equivalent to condition $F_p||C_j$. It ensues from the condition of collinearity of vectors that their components are proportional:

$$f_i=hc_{ji} \text{ and } d_j=\sum hc_{ji}^2,$$

where h is the coefficient of proportionality. Since coding by channel number is equivalent to coding by direction of the excitation vector, instead of vector F_p that is arbitrary with regard to modulus, we shall consider normalized vector $\mathcal{F} = F/|F|$. In this case, $d_{j\max}$ = const for all secondary detectors, i.e.,

$$\sum_{i=1}^{n} c_{ji}^2=\frac{d_j}{h}=r^2=|\mathbf{C}_j|^2$$

or

$$\sum_{i=1}^{n}(c_{ji}/r)^2=1,$$

where $(c_{ji}/r) = \cos \alpha_i$; α_i is the angle between communication vector and ith coordinate axis; $\cos \alpha_i$ is the direction cosine.

Thus, the components of the communication vector are cosine curves. In view of the fact that there is a collinear excitation vector corresponding to each communication vector, we can observe that signals passing to inputs must also be cosine curves.

Subjective gauge of closeness of two stimuli and spherical model. Let there be two stimuli, S_p and S_q, the subjective value of whose parameters is determined by the direction of the corresponding excitation vectors, F_p and F_q. It is logical to assume that stimuli S_p and S_q are subjectively perceived as being increasingly different as angle F_p, F_q increases. It is assumed that the measure [or gauge] of closeness $\psi(S_p, S_q)$ of two stimuli is the angle between the excitation vectors that correspond to these stimuli:

$$\psi[S_p,\ S_q]=\arccos\frac{(\mathbf{F}_p,\ \mathbf{F}_q)}{|\mathbf{F}_p||\mathbf{F}_q|}.$$

If we consider, instead of vectors F the unit vectors $F/|F|$, ϕ = const, the length of the arc (length of geodesic line) connecting two points on a unit sphere, in which are represented the corresponding secondary detectors, could serve as a measure of closeness of two stimuli. For stimuli S_p and S_q, these points are the intersection of the unit sphere with vectors $\mathcal{F}_p = F_p/|F_p|$ and $\mathcal{F}_q = F_q/|F_q|$. Here, $\psi(S_p, S_q) = \cup S_p, S_q$. Subjective space meets the axioms of metric space:

$$1)\ \psi[\mathcal{F}_p, \mathcal{F}_q] = 0 \text{ when and only when } \mathcal{F}_p = \mathcal{F}_q;$$

$$2)\ \psi[\mathcal{F}_p, \mathcal{F}_q] = \psi[\mathcal{F}_q, \mathcal{F}_p];$$

$$3)\ \psi[\mathcal{F}_p, \mathcal{F}_r] \leqslant \psi[\mathcal{F}_p, \mathcal{F}_q] + \psi[\mathcal{F}_q, \mathcal{F}_r].$$

The first two requirements are obvious, while the third axiom is satisfied by virtue of the fact that $\psi[\mathcal{F}_p, \mathcal{F}_r]$ is the length of the geodesic line that connects two points on the sphere.

Criterion of sensitivity of the analyzer to change in coded parameter. Let there be a set of n linearly independent functions in Euclidean space:

$$\{f_i^*(\varphi)\}, \quad (i = 1, \ldots, n), \tag{1.1}$$

which describe the sensitivity of primary detectors, where ϕ is a number that assumes an arbitrary value in the range of $\phi \in L = [\phi_0, \phi_l]$. It is assumed that functions (1.1) in a certain orthogonal basis describe the components of an n-dimensional excitation vector $F(\phi)$. Let there also be given another vector $F(\phi+\tau)$, where τ is a low constant value. With fixed $\phi \in L$, let us determine the quantity

$$\delta = \frac{\sum^{n} f_i^*(\varphi) f_i^*(\varphi+\tau)}{\left[\sum^{n} f_i^{*2}(\varphi) \sum f_i^{*2}(\varphi+\tau)\right]^{1/2}} = \delta(\varphi, \tau). \tag{1.2}$$

Quantity $\delta(\phi, \tau)$ is the cosine of the angle between vectors $F(\phi)$ and $F(\phi+\tau)$, whose coordinates are the numerical values of functions $\{f_i^*(\phi)\}$ and $\{f_i^*(\phi+\tau)\}$ with $\phi \in L$. It is assumed that τ is a small enough quantity for which $\delta(\phi, \tau) \geqslant 0$ is satisfied with any $\phi \in L$.

Equation (1.2) depends on the angle between vectors $F(\phi)$ and $F(\phi+\tau)$: the larger angle $F(\phi)$, $F(\phi+\tau)$, the smaller the value of $\delta(\phi, \tau)$. In turn, sensitivity of the system to a change in parameter ϕ, from ϕ to $\phi+\tau$ will be all the greater, the greater the difference in directions of vectors $F(\phi)$ and $F(\phi+\tau)$, i.e., the larger angle $F(\phi)$, $F(\phi+\tau)$. Consequently, the smaller the value of equation (1.2), the greater the sensitivity of the system at point $\phi \in [f_0, f_l]$. If we know the sensitivity of the system at point ϕ, we can also determine its mean sensitivity over the entire range of $[\phi_0, \phi_l]$. For this, it is sufficient to find the mean value of $\delta(\phi, \tau)$ in interval $[\phi_0, \phi_l]$, i.e.,

$$\eta^*(f_i^*(\varphi)) = \frac{1}{|\varphi_l - \varphi_0|} \int_{\varphi_0}^{\varphi_l} \delta(\varphi, \tau)\, d\varphi. \tag{1.3}$$

In executing the model, it is desirable to select primary detectors that would give the model maximum average sensitivity. For this purpose, one must find a class of functions $\{f_i^*(\phi)\}$ describing sensitivity of primary detectors so that the value of the functional (1.2) of this class of functions would be minimal.

Evidently, the value of functional (1.2) will not change if, instead of vectors $F(\phi)$ and $F(\phi+\tau)$ that are arbitrary in modulus, we consider unit vectors $\mathcal{F}(\phi)$ and $\mathcal{F}(\phi+\tau)$ collinear with vectors $F(\phi)$ and $F(\phi+\tau)$, respectively. The numbers $\{f_i(\phi)\}$ and $\{f_i(\phi+\tau)\}$, $\phi\in[\phi_0, \phi_l]$ serve as coordinates of vectors $\mathcal{F}(\phi)$ and $\mathcal{F}(\phi+\tau)$, and it is assumed that

$$\sum^{n} f_i^2(\varphi)=\sum^{n} f_i^2(\varphi+\tau)=1. \qquad (1.4)$$

Since the modulus of vectors $\mathcal{F}(\phi)$ and $\mathcal{F}(\phi+\tau)$ equals 1 (with given value of $\phi\in L$), sensitivity of the system will be determined by the value of the functional

$$\eta(f_i(\varphi))=\frac{1}{|\varphi_l-\varphi_0|}\int_{\varphi_0}^{\varphi_l}\sum^{n} f_i(\varphi)\,f_i(\varphi+\tau)\,d\varphi, \qquad (1.5)$$

where

$$\sum^{n} f_i(\varphi)\,f_i(\varphi+\tau)$$

is the scalar product of the unit vectors $\mathcal{F}(\phi)$ and $\mathcal{F}(\phi+\tau)$ with a fixed value of ϕ. In this case, we have the problem for an arbitrary extremum: we have to find functions $\{f_i(\phi)\}$ in such a form that in the class of these functions functional (1.5) would be minimal and satisfy condition (1.4) also. In order to solve this problem, we must find such a class of functions, for which functional

$$\eta(f_i(\varphi))=\int_{\varphi_0}^{\varphi_l}\Big\{\sum^{n} f_i(\varphi)\,f_i(\varphi+\tau)-\lambda_1\Big[\sum^{n} f_i^2(\varphi)-1\Big]- -\lambda_2\Big[\sum^{n} f_i^2(\varphi+\tau)-1\Big]\Big\}\,d\varphi \qquad (1.5a)$$

((λ_1, λ_2) -- Lagrange factors) would be minimal.

A mandatory condition for extremization by functions

$$\{f_i(\varphi)\},\quad (i=1,\ldots,n), \qquad (1.6)$$

of functional (1.5a) is that they must satisfy the system of Euler's equations. In the case of a variational problem with shifted argument, the system of Euler equations has the following appearance [103]:

$$\Phi_{f_i}-\frac{d}{d\varphi}\Phi_{f_i}+\tilde{\Phi}_{f_i}-\frac{d}{d\varphi}\tilde{\Phi}_{f_i}=0, \qquad (1.7)$$

where Φ is the expression of functional (1.5a) under the integral sign; $\tilde{\Phi}$ is what is obtained from Φ with substitution of variable $\tilde{\phi} = \phi + \tau$; Φ_{f_i} and $\tilde{\Phi}_{f_i}$ are partial derivatives of Φ and $\tilde{\Phi}$ for an independent variable $f_i(\phi)$ or $f_i(\tilde{\phi})$, respectively, Φ'_{f_i} and $\tilde{\Phi}'_{f_i}$ are analogous partial derivatives taken according to $f_i(\phi)$ and $f_i(\tilde{\phi})$.

Since functional (1.5a) is unrelated to $f_i(\phi)$, equation (1.7) has the following appearance:

$$\Phi_{f_i}+\tilde{\Phi}_{f_i}=0, \quad (i=1,\ldots,n). \tag{1.7a}$$

In addition, function (1.6) must satisfy the following conditions at the ends of interval $[\phi_0, \phi_l]$:

$$\begin{aligned} f_i(\varphi)&=a_i(\varphi) \text{ with } \varphi\in[\varphi_0, \varphi_0+\tau], \\ f_i(\varphi)&=b_i(\varphi) \text{ with } \varphi\in[\varphi_l, \varphi_l+\tau], \end{aligned} \tag{1.7b}$$

where $a_i(\phi)$ and $b_i(\phi)$ are certain known functions. Conditions (1.7b) are analogous to boundary conditions in the usual variational problem with fixed ends [103].

For (1.5a), the system of Euler equations has the following appearance:

$$\begin{aligned} f_i(\varphi+\tau)-2\lambda_1 f_i(\varphi)+f_i(\varphi-\tau)-2\lambda_2 f_i(\varphi)&=0, \\ f_i(\varphi+\tau)+f_i(\varphi-\tau)&=\lambda^* f_i(\varphi), \end{aligned} \tag{1.8}$$

where $\lambda^*=2(\lambda_1+\lambda_2)$

From (1.8) we get:

$$f_i(\varphi)=[f_i(\varphi+\tau)+f_i(\varphi-\tau)]/\lambda^*. \tag{1.9}$$

From condition $\sum_i^n f_i^2(\phi)=1$, it is not difficult to obtain the value of λ^* and, after inserting the obtained expression in (1.9) we finally get:

$$f_i(\varphi)=\frac{f_i(\varphi+\tau)+f_i(\varphi-\tau)}{\{\sum[f_i(\varphi+\tau)+f_i(\varphi-\tau)]^2\}^{1/2}}. \tag{1.10}$$

Since the denominator in the right part of (1.10) does not depend on i, equation (1.10) can be written in a somewhat different form:

$$f_i(\varphi)=\frac{1}{a(\varphi,\tau)}[f_i(\varphi+\tau)+f_i(\varphi-\tau)],$$

where

$$a(\varphi,\tau)=\{\sum[f_i(\varphi+\tau)+f_i(\varphi-\tau)]^2\}^{1/2},$$

or in vector form

$$\mathscr{F}(\varphi)=\frac{1}{a(\varphi,\tau)}[\mathscr{F}(\varphi+\tau)+\mathscr{F}(\varphi-\tau)]. \tag{1.11}$$

According to (1.11), any three excitation vectors found in three points, ϕ, $\phi+\tau$, $\phi-\tau$, $(\phi\in[\phi_0, \phi_l])$, are linearly dependent. Consequently, extremal $\{f_i(\phi)\}\phi\in[\phi_0, \phi_l]$ is a flat curve, i.e., it is in a certain two-dimensional plane.

Thus, the proposed method for coding parameter ϕ, which assumes an arbitrary value in the interval $[\phi_0, \phi_l]$, involves reflection of interval $[\phi_0, \phi_l]$ on the circumference. Each point on the circumference is characterized by two coordinates, i.e., in this case the minimum number of functions (1.10) is two. By substituting the value in (1.10):

$$f_1(\varphi) = \cos\lambda\varphi \text{ and } f_2(\varphi) = \sin\lambda\varphi, \quad \lambda = \text{const}, \tag{1.12}$$

we get an identity.

It should be noted that (1.10) also satisfies the functions

$$f_1(\varphi) = \cos f(\varphi) \text{ and } f_2(\varphi) = \sin f(\varphi),$$

$f(\varphi)$ is a monotonic function, and $f(\varphi + r) \cong f(\varphi) + rf'(\varphi)$.

The larger λ is, the greater the sensitivity of the system to a change in parameter ϕ (see expression (1.12)). From the requirement of unambiguous reflection of interval $[\phi_0, \phi_l]$ on the circle (two-dimensional plane), the value of λ is restricted. With change in parameter ϕ from ϕ_0 to ϕ_l, the direction of the excitation vector can change from 0 to 2π: with great changes in direction of the vector, different points of interval $[\phi_0, \phi_l]$ will correspond to the same point on the circle [circumference]. Thus,

$$\arccos\cos[\mathscr{F}(\varphi_0), \mathscr{F}(\varphi_l)] = \arccos\cos\lambda(\varphi_0 - \varphi_l) = 2\pi,$$

i.e., the maximum value of λ is:

$$\lambda = 2\pi/(\varphi_l - \varphi_0).$$

The question arises as to whether one can increase sensitivity of the system without disrupting the unambiguity [single value?] of the above-mentioned reflection. We find that this can be done; however, the dimensionality of space in which parameter $\phi \in [\phi_0, \phi_l]$ is reflected must be increased. Let the entire possible range $[\phi_0, \phi_l]$ of values of parameter ϕ be separated into k mutually nonoverlapping segments $[\phi_0, \phi_1]$, $[\phi_1, \phi_2]$, ..., $[\phi_{i-1}, \phi_i]$, ..., $[\phi_{k-1}\ \phi_l]$. Points on the ends of segments belong to two adjacent intervals simultaneously, $[\phi_{i-2}, \phi_{i-1}]$ and $[\phi_{i-1}, \phi_i]$. We shall then consider these segments as intervals of values k of independent variables $\phi_i' \in [\phi_{i-1}, \phi_i]$, $(i = 1, \ldots, k)$, each of which is reflected on its own separate plane. Ultimately, we have k separate planes, the mutual position of which in space is not defined. For such a reflection to satisfy the condition of unambiguity, each point over the entire range $[\phi_0, \phi_l]$ must correspond to one and only one point in space. Since two adjacent intervals $[\phi_{i-2}, \phi_{i-1}]$ and $[\phi_{i-1}, \phi_i]$ have a common point ϕ_{i-1}, this point in space corresponds to the same unit vector $\mathscr{F}(\phi)$. Consequently, the regions of planes, in which parameters ϕ_{i-1}' and ϕ_i' are reflected, must have one and only one common point on the line of intersection of these planes.

As a graphic illustration, let us consider a concrete case of such reflection. Let the interval $[\phi_0, \phi_l]$ of values of ϕ be separated into three equal segments $[\phi_0, \phi_1]$, $[\phi_1, \phi_2]$ and $[\phi_2, \phi_l]$.

We then construct the next functions, considering that $\lambda = 3\pi/(\phi_l - \phi_0)$ and $\phi^* = \phi - \phi_0$:

$$f_1(\varphi)=\begin{cases} |\cos\lambda\varphi^*|, & \text{if } \varphi\in[\varphi_0,\ (\varphi_0+\varphi_1)/2]\cup[(\varphi_l+\varphi_2)/2,\ \varphi_l]; \\ -|\sin\lambda\varphi^*|, & \text{if } \varphi\in[\varphi_1,\ \varphi_2]; \\ 0 \text{— in the other cases.} \end{cases}$$

$$f_2(\varphi)=\begin{cases} |\sin\lambda\varphi^*|, & \text{if } \varphi\in[\varphi_0,\ \varphi_1]; \\ -|\cos\lambda\varphi^*|, & \text{if } \varphi\in[(\varphi_1+\varphi_2)/2,\ (\varphi_2+\varphi_l)/2]; \quad \cancel{(1.10)} \\ 0 \text{— in the other cases} \end{cases} \tag{1.13}$$

$$f_3(\varphi)=\begin{cases} |\cos\lambda\varphi^*|, & \text{if } \varphi\in[(\varphi_0+\varphi_1)/2,\ (\varphi_1+\varphi_2)/2]; \\ -|\sin\lambda\varphi^*|, & \text{if } \varphi\in[\varphi_2,\ \varphi_l]; \\ 0 \text{—in the other cases.} \end{cases}$$

Functions (1.13), which correspond to the sensitivity characteristics of primary detectors, apparently satisfy the optimality conditions (1.10).

In this case, parameter $\phi\in[\phi_0,\ \phi_l]$ is reflected on three mutually orthogonal planes. If an orthonormal basis e_1, e_2, e_3 is given and functions (1.13) are considered as components of a certain three-dimensional vector $\mathcal{F}(\phi)$ in this space, with a change in parameter ϕ from ϕ_0 to $(\phi_0+\phi_1)/2$, vector $\mathcal{F}(\phi)$ traces a circle, turning from vector e_1 to $e_2 (e_1 \to e_2)$. Further increase in ϕ from $(\phi_0+\phi_1)/2$ to ϕ_1 leads to continuous rotation of vector $\mathcal{F}(\phi)$: $e_2 \to e_3$, and with change of ϕ in the interval:

$$[\varphi_1,\ (\varphi_1+\varphi_2)/2] - -e_3 \to -e_1,\quad \varphi\in[(\varphi_1+\varphi_2)/2,\ \varphi_2] - e_1 \to -e_2,$$
$$\varphi\in[\varphi_2,\ (\varphi_2+\varphi_l)/2] - -e_2 \to -e_3 \text{ и}$$
$$\varphi\in[(\varphi_2+\varphi_l)/2,\ \varphi_l] - -e_3 \to e_1.$$

As a result of the above-described reflection, the total turn of the excitation vector with change in ϕ from $\phi_0 \to \phi_l$ will constitute 540°, which is 1.5 times more than in the case where $\lambda = 2$. By continuing to increase the number k of subintervals that are reflected on their own planes, we shall increasingly narrow functions (1.13). Concurrently, there will be an increase in λ. Within the limit, functions (1.13) become deltoid and excitation vector F_p assumes the appearance of $\{\ldots,\ 0,\ \pm1,\ 0,\ 0,\ \ldots\}$.

Characteristics of secondary detectors. According to the foregoing, in building the model, to each secondary detector is assigned a certain communication vector C_j, which is collinear with a specific excitation vector $\mathcal{F}(\phi)$, $\phi = \phi_p$, and $|C_j| = \text{const}$. We can then determine the distribution of excitation on the set of secondary detectors:

$$d(k,\ \varphi_p) = c_{k1} f_1(\varphi_p) + c_{k2} f_2(\varphi_p). \tag{1.14}$$

Substituting their values for c_{ki}, $(i = 1,\ 2;\ l = 1,\ \ldots,\ m)$, and $f_i(\phi)$, we get:

$$d(k,\ \varphi_p)=h\cos f(\varphi_k)\cos f(\varphi_p)+h\sin f(\varphi_k)\sin f(\varphi_p) \tag{1.15}$$

or

$$d(k,\ \varphi_p)=h\cos[f(\varphi_k)-f(\varphi_p)], \tag{1.16}$$

$$\varphi_p=\text{const},\ \varphi_k=[\varphi_0,\ \varphi_l].$$

The value of ϕ_k is different for each secondary detector.

Analogously, we can find the reaction of an individual detector as a function of value of parameter $\phi \in [\phi_0,\ \phi_l]$:

$$d(j,\ \varphi)=f_0(\varphi)=c_{j1}f_1(\varphi)+c_{j2}f_2(\varphi),\quad j=\text{const}, \tag{1.17}$$

or

$$d(j,\ \varphi_p)=c\cos[f(\varphi)-f(\varphi_j)].$$

In conclusion, it should be noted that the proposed method of building secondary detectors is not the only one, since condition $|C_j| = \text{const}$ ($j = 1, \ldots, m$) is not mandatory. Let us consider a variant of separate channels for excitation and inhibition. Let there be a set of four primary detectors with the following sensitivity characteristics:

$$\begin{aligned}
f_1(\varphi)&=\begin{cases}\cos f(\varphi), & \text{if } -\pi/2\leqslant f(\varphi)\leqslant\pi/2;\\ 0, & \text{if } \pi/2\leqslant f(\varphi)\leqslant\frac{3}{2}\pi;\end{cases}\\
f_2(\varphi)&=\begin{cases}0, & \text{if } -\pi/2\leqslant f(\varphi)\leqslant\pi/2;\\ -\cos f(\varphi), & \text{if } \pi/2\leqslant f(\varphi)\leqslant\frac{3}{2}\pi;\end{cases}\\
f_3(\varphi)&=\begin{cases}\sin f(\varphi), & \text{if } 0\leqslant f(\varphi)\leqslant\pi;\\ 0, & \text{if } \pi\leqslant f(\varphi)\leqslant 2\pi;\end{cases}\\
f_4(\varphi)&=\begin{cases}0, & \text{if } 0\leqslant f(\varphi)\leqslant\pi;\\ -\sin f(\varphi), & \text{if } \pi\leqslant f(\varphi)\leqslant 2\pi,\end{cases}
\end{aligned} \tag{1.18}$$

where functions $f_1(\phi)$ and $f_2(\phi)$ together realize $|\cos f(\phi)|$, $f_1(\phi)$ realizing the positive cosine curve period and $f_2(\phi)$ the negative one. The same applies to functions $f_3(\phi)$ and $f_4(\phi)$, which together realize the sine curve.

If there are four primary detectors, there are two ways of constructing secondary detectors. In the first case, each secondary detector supplied with a communication vector is collinear to the excitation vector:

$$c_{j1}=h\cos f(\varphi_j)\ \text{and}\ c_{j2}=h\sin f(\varphi_j),$$

$$\varphi_j\in[\varphi_0,\ \varphi_l].$$

If, with a given value of parameter $\phi = \phi_j$ the value of the cosine (sine) curve is negative, the secondary detector receives excitation from the second (or fourth) primary detector and inhibition from the odd-numbered primary detector. The absolute value of connections between the first and second (third, fourth) primary detectors with the secondary detectors is equal.

If, however, with $\phi = \phi_j$, the cosine (sine) curves are positive, the secondary detector receives excitation from the first (third) and inhibition from the second (fourth) primary detectors, the magnitude of connections from the first, second (third, fourth) primary detectors being equal in absolute value.

With such construction of secondary detectors, all of their characteristics remain the same as in the case where there were combined channels for transmission of excitation and inhibition.

If, in the case we have just discussed for construction of secondary detectors, we were to discard all inhibitory connections between primary and secondary detectors and retain the excitatory ones, we obtain the second method of executing a model that codes the parameter by the number of the output element with maximum excitation. In this case, there is a change in characteristics of secondary detectors (the inhibitory "drift" disappears); however, this does not affect the principle of coding with channel number, since the position of the excitation maximum on the population of detectors does not change.

Adaptation in the system of primary detectors. Differential sensitivity of analyzer: Let us consider the conditions, under which adaptation to stimulus S_ϕ (lowering of excitation level during prolonged viewing of stimulus S_ϕ) enhances differential sensitivity of the system to a change in this stimulus.

Adaptation leads to some transformation of excitation vector $\mathscr{F}(\phi)$. Instead of $\mathscr{F}(\phi)$, the excitation vector becomes:

$$\mathbf{F}(\varphi/\varphi_a) = \mathscr{A}(\varphi_a, t)\,\mathscr{F}(\varphi), \tag{1.19}$$

where $\mathscr{A}(\phi_a, t)$ is a certain operator that depends on both the value of parameter ϕ_a of adapting stimulus S_{ϕ_a} and on time t, during which this stimulus is presented. Vector $F(\phi/\phi_a)$ is the excitation vector generated by stimulus S_ϕ, with consideration of prior adaptation to stimulus S_{ϕ_a}. Stimulus S_ϕ is presented to the system immediately after adaptive stimulus S_{ϕ_a}.

Let operator $\mathscr{A}(\phi_a, t)$ have the following appearance:

$$\mathscr{A}(\varphi_a, t) = \|(1 - \gamma(t)\,|f_i(\varphi_a)|)\,\delta_{ij}\|, \tag{1.20}$$

where $\gamma(t)$ is a certain function that does not diminish in time, and $1 \geqslant \gamma(t) \geqslant 0 = \gamma(0)$; $\{f_i(\phi_a)\}$, $(i = 1, \ldots, n)$ are components of excitation vector $\mathscr{F}(\phi_a)$; δ_{ij} is Kronecker's delta symbol ($\delta_{ij} = 1$, if $i = j$, and $\delta_{ij} = 0$ with $i \neq j$).

The physical meaning of operator (1.20) is that, under the influence of adapting stimulus S_{ϕ_a}, the longer and greater the absolute excitation of this detector, the more marked the decline in sensitivity of primary detectors.

In (1.20), the decline of sensitivity of primary detectors depends on the absolute level of its excitation. This is based on the assumption that the same primary detector is excitatory for some secondary detectors and inhibitory for others.

Let us see how differential sensitivity of the system changes under the influence of adaptation. In order to determine differential sensitivity, we must find out how the subjective distance between two stimuli S_ϕ and $S_{\phi+\tau}$, where τ is a rather small constant, $\phi\in[\phi_0, \phi_l]$, changes under the influence of adaptation. As we have indicated, the subjective distance between stimuli equals the angle between the excitation vectors corresponding to these stimuli, i.e.,

$$\psi^* = [\overline{F((\varphi+\tau)/\varphi_a)},\ \overline{F(\varphi/\varphi_a)}], \quad (1.21)$$
$$\tau,\ \varphi_a = \mathrm{const},\quad \varphi\in[\varphi_0, \varphi_l].$$

Without adaptation, the subjective distance between the same stimuli, S_ϕ and $S_{\phi+\tau}$, is determined by the angle:

$$\psi = \overline{\mathscr{F}(\varphi+\tau)},\ \overline{\mathscr{F}(\varphi)}. \quad (1.21)$$

Here, ψ is the distance between stimuli before adaptation and ψ^* after adaptation.

Thus, the difference

$$\Delta\psi = \psi^* - \psi \quad (1.22)$$

determines how the subjective distance between two stimuli changes under the influence of adaptation. If (1.22) is positive, adaptation for the given values of parameter ψ increases differential sensitivity of the analyzer, and if it is negative, it decreases this sensitivity [40, 102].

This increase in differential sensitivity under the influence of adaptation can be found analytically.

Figure 15 shows that, as a result of adaptation, differential sensitivity of the analyzer to stimuli that are similar to the adaptive stimulus increases ($\Delta\psi>0$). A maximum increase in sensitivity is obtained when the adaptive stimulus corresponds to the following values for the argument of the cosine curve that describe the sensitivity of primary detectors:

$$f(\varphi) = 0, 90, 180, 270^\circ \quad (1.23)$$

and differential sensitivity does not change under the influence of adaptation if:

$$f(\varphi) = 45, 135, 225, 315^\circ. \quad (1.23a)$$

Such an increase in analyzer sensitivity is useful from the functional point of view: during prolonged viewing of the same stimulus there is an increase in the system's capacity to detect minor deviations from the adapting stimulus.

It should be noted that if the sensitivity of primary detectors increases during adaptation, the differential sensitivity of the analyzer to stimuli close to the adaptive one, on the contrary, diminishes $\Delta\psi<0$.

Adaptation effects: Let there be a certain stimulus S_ϕ, which generates excitation vector $\mathscr{F}(\phi)$. Let also operator $\mathscr{A}(\phi, t)$ (1.19) describe the change in sensitivity of primary detectors under the influence of this stimulus. Thus, under the prolonged effect of stimulus S_ϕ the excitation vector can be found from the following expression, $F(\phi/\phi_a) = \mathcal{A}(\phi, t)\ \mathcal{F}(\phi)$. In the general case, after adaptation the excitation vector does not coincide in direction with the excitation vector that corresponds to the stimulus before adaptation. The question arises, in which cases does the excitation vector remain collinear after adaptation to the vector of excitation before adaptation. For this, one has to find the values of parameter that correspond to the eigen vectors of operator $\mathcal{A}(\phi, t)$.

Let us find the conditions under which the following equality is satisfied:

$$F(\varphi/\varphi) = \lambda\mathcal{F}(\varphi) = \mathcal{A}(\varphi, t)\mathcal{F}(\varphi), \qquad (1.24)$$

where λ are the eigen numbers of operator $\mathcal{A}(\phi, t)$.

Considering the form of operator $\mathcal{A}(\phi, t)$ (1.19), it is not difficult to obtain

$$\lambda_k = 1 - \gamma(t)|f_k(\varphi)|. \qquad (1.25)$$

In order to determine the eigen vectors of operator $\mathcal{A}(\phi, t)$, we insert the obtained values of eigen numbers in (1.24), where we obtain after simple conversions:

$$f_i(\varphi)(|f_i(\varphi)| - |f_k(\varphi)|) = 0. \qquad (1.26)$$

This condition means that for vector $\mathcal{F}(\phi)$ to be the eigen vector of operator $\mathcal{A}(\phi, t)$ there must be the condition of identity of its nonzero components with regard to absolute value at any point in time.

If stimulus S_ϕ does not correspond to the eigen vector of operator $\mathcal{A}(\phi, t)$, it changes continuously in the course of adaptation. The speed of adaptation depends on function $\gamma(t)$ (see (1.20)): the faster function $\gamma(t)$ increases in time, the faster the subjective drift of stimulus S_ϕ. The drift is always in the direction of one of the invariant (independent of adaptation) values of parameter ϕ of stimulus S_ϕ.

Thus, the normalization effect is the consequence of adaptation of the (1.20) type on the level of primary detectors. In psychophysics, constant drift of perception of an adaptive stimulus is known as the normalization effect.

Let stimulus S_ϕ generate vector $\mathcal{F}(\phi)$ before adaptation to stimulus $S\phi_a$ and vector $F(\phi/\phi_a)$ (1.19) after adaptation. If the two vectors are collinear to one another, S_ϕ is perceived identically both before and after adaptation. If the vectors are not collinear, the same stimulus S_ϕ is perceived as two different stimuli before and after adaptation. The subjective distance between these stimuli is determined by the angle between vectors $\mathcal{F}(\phi)$ and $F(\phi/\phi_a)$, i.e.,

$$\mathcal{F}(\varphi),\ F(\varphi/\varphi_a). \qquad (1.27)$$

In the literature, the above effect is known as the aftereffect.

Interaction between two local analyzers: In a real situation, there is often the problem of determining equality of two simultaneously delivered stimuli. Let us consider the conditions, under which one can increase the system's capacity to distinguish between two stimuli.

Type of interaction that enhances discrimination: Let us consider two separate local analyzers. The receptive fields of these analyzers cover the space of different sensory areas. Stimulus S_{ϕ_k} is delivered to one analyzer and S_{ϕ_m} to the other. These stimuli correspond to excitation vectors $\mathcal{F}(\phi_k)$ and $\mathcal{F}(\phi_m)$. Let us insert between these analyzers the interaction described by operator A. With consideration of interaction A, instead of excitation vectors $\mathcal{F}(\phi_k)$ and $\mathcal{F}(\phi_m)$, we shall have the following vectors:

$$\mathbf{F}(\varphi_k) = \mathcal{F}(\varphi_k) - A\mathcal{F}(\varphi_m), \tag{1.28}$$

$$\mathbf{F}(\varphi_m) = \mathcal{F}(\varphi_k) - A\mathcal{F}(\varphi_k). \tag{1.29}$$

The question arises as to what operator A must be so that the analyzer of parameter ϕ would have the following properties.

1. If stimuli S_{ϕ_k} and S_{ϕ_m}, which have the same parameter ϕ, i.e., $\phi_k = \phi_m$, are delivered separately to the input of interacting analyzers, as a result of interaction A the subjectively perceived value of parameters ϕ_k and ϕ_m should not change, remaining the same as without interaction. This means that if two identical stimuli are delivered simultaneously, as a result of interaction these stimuli should be perceived not only as being identical, but the same as in the absence of interaction. Thus, if excitation vectors $\mathcal{F}(\phi_k)$ and $\mathcal{F}(\phi_m)$ are collinear, vectors $F(\phi_k)$ and $F(\phi_m)$ must not only be collinear [to one another], but have the same direction as vectors $\mathcal{F}(\phi_k)$ and $\mathcal{F}(\phi_m)$:

$$\mathcal{F}(\varphi_k) \| \mathcal{F}(\varphi_m) \| \mathbf{F}(\varphi_k) \| \mathbf{F}(\varphi_m). \tag{1.30}$$

2. If the difference between values of parameters of the two stimuli S_{ϕ_k} and S_{ϕ_m} is small, i.e., $\Delta\phi = |\phi_k - \phi_m|$ is small, as a result of interaction the subjective difference between stimuli should increase. This means that the angle between vectors $F(\phi_k)$ and $F(\phi_m)$ must be larger than the angle between vectors $\mathcal{F}(\phi_k)$ and $\mathcal{F}(\phi_m)$:

$$\mathbf{F}(\varphi_k),\ \mathbf{F}(\varphi_m) - \mathcal{F}(\varphi_k),\ \mathcal{F}(\varphi_m) > 0. \tag{1.31}$$

In the case where condition (1.30) is satisfied, i.e., $\mathcal{F}(\phi_k) = \mathcal{F}(\phi_m) = \beta F(\phi_k) = \beta F(\phi_m)$, one can rewrite expression (1.29) in the following form:

$$\mathcal{F}(\varphi_k)/\beta = \mathcal{F}(\varphi_k) - A\mathcal{F}(\varphi_m) \tag{1.32}$$

or

$$(1 - 1/\beta)\mathcal{F}(\varphi_k) = A\mathcal{F}(\varphi_m) = A\mathcal{F}(\varphi_k), \tag{1.33}$$

where vector $\mathcal{F}(\phi_k)$ is the eigen vector of operator A.

Since $\mathcal{F}(\phi_k)$ is an arbitrary vector, condition (1.33) is satisfied if operator A is diagonal, and the following coefficients are on the main diagonal:

$$a_{ii} = \alpha = 1 - 1/\beta. \tag{1.34}$$

From condition (1.31), it is not difficult to find the sign and value of coefficient α. For interaction between analyzers to increase differential sensitivity it is necessary to have $1 \geqslant \alpha \geqslant 0$.

Differential sensitivity and value of coefficient α: As a graphic illustration, let us consider a two-dimensional case. Let there be two vectors $\mathcal{F}(\phi_k)$ and $\mathcal{F}(\phi_m)$ with components

$$\{\cos f(\varphi_k),\ \sin f(\varphi_k)\} \text{ и } \{\cos f(\varphi_m),\ \sin f(\varphi_m)\}. \tag{1.35}$$

As a result of the previously discussed interaction, vectors (1.35) assume the following appearance:

$$\begin{aligned}&\{\cos f(\varphi_k) - \alpha\cos f(\varphi_m),\ \sin f(\varphi_k) - \alpha\sin f(\varphi_m)\},\\&\{\cos f(\varphi_m) - \alpha\cos f(\varphi_k),\ \sin f(\varphi_m) - \alpha\sin f(\varphi_k)\}.\end{aligned} \tag{1.36}$$

Let us use (1.36) to determine the angle between vectors $F(\phi_k)$ and $F(\phi_m)$. For this, let us find the cosine of this angle:

$$\cos[\mathbf{F}(\varphi_k),\ \mathbf{F}(\varphi_m)] = \frac{(1+\alpha^2)\cos\Delta\varphi - 2\alpha}{1+\alpha^2 - 2\alpha\cos\Delta\varphi}, \tag{1.37}$$

where $\Delta\phi = |f(\phi_m) - f(\phi_k)|$, and then the angle:

$$\mathbf{F}(\varphi_k),\ \mathbf{F}(\varphi_m) = \arccos\left[\frac{(1+\alpha^2)\cos\Delta\varphi - 2\alpha}{1+\alpha^2 - 2\alpha\cos\Delta\varphi}\right]. \tag{1.38}$$

If, as a result of interaction, there was subjective increase in distance between stimuli, angle $F(\phi_k)$, $F(\phi_m)$ will be larger than angle $\mathcal{F}(\phi_k)$, $\mathcal{F}(\phi_m)$:

$$\Delta\psi_1 = \mathbf{F}(\varphi_k),\ \mathbf{F}(\varphi_m) - \Delta\varphi > 0. \tag{1.39}$$

At what values of difference $\Delta\phi$ does function $\Delta\psi_1$ reach a maximum value? Let us differentiate function (1.39) in relation to $\cos\Delta\phi$:

$$\frac{\partial\Delta\psi_1}{\partial\cos\Delta\varphi} = \frac{2\alpha(\alpha - \cos\Delta\varphi)}{\sin\Delta\varphi(1+\alpha^2 - 2\alpha\cos\Delta\varphi)}.$$

Condition $\partial\Delta\psi_1/\partial\cos\Delta\phi = 0$ is satisfied at values of $\Delta\phi$ when the following equality applies:

$$\alpha = \cos\Delta\phi \text{ or } \Delta\phi = \arccos\alpha \tag{1.40}$$

Thus, the closer α is to one, the lower the values of $\Delta\phi$ with which function (1.39) assumes a maximum value.

Reaction of secondary detectors as a function of magnitude of interaction of coefficient α and difference $\Delta\phi$: The output signal of the jth secondary detector is $d(j, \phi) = (C_j, \mathcal{F}(\phi))$. With consideration of interaction (1.30):

$$d(j,\ \varphi) = (\mathbf{C}_j,\ \mathcal{F}(\varphi) - \alpha\mathcal{F}(\varphi_m)), \tag{1.41}$$

where ϕ_m, $\phi \in [\phi_0, \phi_l]_\phi$ is the parameter of the stimulus delivered to the analyzer in question, while ϕ_m is the parameter of the next one. Let us write (1.41) in a different form: $d(j, \phi) = (C_j, \mathcal{F}(\phi)) - \alpha(C_j, \mathcal{F}(\phi_m)$, or:

$$d(j, \varphi) = \cos[f(\varphi_j) - f(\varphi)] - \alpha \cos[f(\varphi_j) - f(\varphi_m)]. \tag{1.42}$$

$$\text{If} \quad \varphi = \varphi_j = \text{const}, \ \varphi_m \in [\varphi_0, \ \varphi_l] \text{ and } \Delta\varphi = f(\varphi_j) - f(\varphi_m),$$
$$\text{then } d(j, \varphi) = 1 - \alpha \cos \Delta\varphi = f(\Delta\varphi). \tag{1.43}$$

Thus, the jth detector adjusted for stimulus S_{ϕ_j} experiences maximum inhibition by the next [adjacent] analyzer if there are stimuli with the same parameters in the receptive fields of both analyzers.

Interaction of the simultaneous contrast type as a means of providing for invariance. Let two stimuli $S_{\phi k}$ and $S_{\phi m}$ be delivered to the inputs of two analyzers, respectively. Let another stimulus, $S_{\phi\theta}$, act simultaneously on both analyzer inputs. In other words, each of the analyzers sees its stimulus $S_{\phi k}$ or $S_{\phi m}$ on the background of stimulus $S_{\phi\theta}$. Thus, as a result of effects of two stimuli, $S_{\phi k}+S_{\phi\theta}$, we have excitation vector $\mathcal{F}(\phi_k) + \mathcal{F}(\phi_\theta)$ in the first analyzer and $\mathcal{F}(\phi_m) + \mathcal{F}(\phi_\theta)$ in the second one. With consideration of interaction (1.30), we have the following two excitation vectors:

$$\begin{aligned} \mathbf{F}(\varphi_k) &= \mathcal{F}(\varphi_k) - \alpha\mathcal{F}(\varphi_m) + (1\alpha) - \mathcal{F}(\varphi_B), \\ \mathbf{F}(\varphi_m) &= \mathcal{F}(\varphi_m) - \alpha\mathcal{F}(\varphi_k) + (1-\alpha)\mathcal{F}(\varphi_B). \end{aligned} \tag{1.43a}$$

If α is close to one, the influence of the background as a result of interaction is negligible. Interaction of the "simultaneous contrast" type provides for some invariance of perception of the stimulus in relation to the background.

If we consider that, in a real analyzer, many local analyzers interact, the influence of the background could be reduced to nil even with low values of coefficient . Indeed, the background is usually uniformly distributed over all the receptive fields of local analyzers, whereas the discriminated signal is delivered locally. Thus, the inhibitory signal going to a given analyzer from a set of adjacent local analyzers can totally compensate for the influence of the background. In this case, expression (1.43a) is replaced with:

$$\mathbf{F}(\varphi_k) = \mathcal{F}(\varphi_k) - \sum_{R_1} \alpha\mathcal{F}(\varphi_m) - \Big(1 - \sum_{R_1} \alpha\Big)\mathcal{F}(\varphi_B), \tag{1.44}$$

where R_1 is the set of local analyzers affected by stimulus $S_{\phi m}$ and R_2 is the set of analyzers affected by background stimulus $S_{\phi\theta}$.

APPENDIX 2. INTENSITY ANALYZER

Sensitivity characteristics of primary detectors. The local model of an intensity analyzer consists of a layer of photoreceptors, which transform the photic signal into an electrical one, a pair of primary detectors and output secondary detectors. The sensitivity of the receptors [16] is described by:

$$f_r(I) = \mathrm{th}\,\beta I \tag{2.1}$$

In the range of average intensities, we can replace expression (2.1) with:

$$f_r(I) = \log \beta I \tag{2.2}$$

Let the primary detectors have the following sensitivity functions:

$$f_1(I) = \sin \alpha \ \mathrm{th}\,\beta I \tag{2.3}$$

and

$$f_2(I) = \cos \alpha \ \mathrm{th}\,\beta I \tag{2.4}$$

where α and β = const.

Let us call the detector with characteristics of the (2.3) type the B detector (or neuron) and one of the (2.4) type the D detector (or neuron).

With consideration of characteristics $f_1(I)$ and $f_2(I)$ altered by adaptation, we can calculate the angle between the excitation vector of an arbitrary stimulus and the vector of "gray color proper":

$$\psi(I) = [\mathcal{F}(I=0),\ \mathbf{F}(I/I_a)].$$

Functions $\psi(I)$ in the model are an analogue of subjective difference for the function of Stevens.

Let us consider the case where a vector, one component of which equals zero ($\alpha\ \mathrm{th}\,\beta I = 0$), is selected as the zero vector. Then sensitivity to stimuli that are brighter than "eigen gray" increases, whereas the maximum possible subjective distance between stimuli increases to $\pi/2$. However, there is no room in such a model to perceive "black," i.e., stimuli of lesser intensity than the "retina's own light." This flaw can be eliminated by introducing inhibitory connections between homonymous primary detectors of the main and inductive field.

Let us consider the case where the main field is not illuminated and the stimulus is delivered only to the inductive field. Then the signal at the output of the B detector of the main field is:

$$f_1(I) = -\alpha \sin f(I) \tag{2.5}$$

and the one at the output of the D detector is:

$$f_2(I) = 1 - \alpha \cos f(I). \tag{2.5a}$$

After normalization, we have:

$$f_1(I) = -\frac{\alpha \sin f(I)}{[1 + \alpha^2 - 2\alpha \cos f(I)]^{1/2}} \tag{2.6}$$

and

$$f_2(I) = \frac{1 - \alpha \cos f(I)}{[1 + \alpha^2 - 2\alpha \cos f(I)]^{1/2}}. \tag{2.7}$$

The last two expressions can be viewed as functions of primary detector sensitivity when only the inductive field is illuminated and no stimulus is delivered to the main field. In this case, we can speak formally of delivery of a stimulus with negative intensity to the main field. Then expressions (2.6) and (2.7) describe the responses of primary detectors to delivery of a stimulus with negative intensity, which corresponds to blackening.

Thus, when constructing the set of secondary detectors one must also take into consideration negative intensities that correspond to blacks. Formally, there are no difficulties involved in building such detectors: a communication vector with constant modulus, collinear with one of the excitation vectors, including those generated by stimuli with negative intensity, is assigned to each detector.

Weber's ratio in the intensity analyzer. Let there be stimuli S_I and $S_{I+\Delta I}$, to which correspond excitation vectors $\mathcal{F}(I)$ and $\mathcal{F}(I + \Delta I)$, where I is the current intensity of the stimulus and ΔI is the threshold intensity increment.

According to the foregoing, angle

$$\psi = [\overline{\mathcal{F}}(I), \overline{\mathcal{F}}(I + \Delta I)] = \text{const} \tag{2.8}$$

is the angle that determines the distance between two adjacent secondary detectors. Knowing angle ψ (2.8), it is not difficult to determine the following values:

$$\Delta I = z(\psi, I), \tag{2.9}$$

and Weber's ratio will appear as

$$\Delta I / I = z(\psi, I)/I. \tag{2.10}$$

If the density of the detectors is not constant, ψ will be a certain function of I. If this function is known one can determine Weber's ratio, with consideration of the changing threshold.

Adaptation in the intensity analyzer. Adaptation at the input of primary detectors: Let adaptive stimulus S_{I_a} be delivered to the input of the system. A signal is delivered to the input of horizontal cells which equals:

where $P_p(I_a)$ is the receptor's reaction to the adaptive stimulus, R_B is the set of receptors of the main field. If the adaptive stimulus is followed by delivery of stimulus S_I whose intensity is I units, the signal at the input of the primary detectors can be calculated as follows:

$$f_1(I)=\begin{cases}\sin \alpha u(I), & \text{if } u(I)=\sum\limits_{R_B} P_p(I)-\beta\sum\limits_{R_B} P_p(I_a)>0,\\ 0, & \text{if } u(I)\leqslant 0;\end{cases} \tag{2.11}$$

$$f_2(I)=\begin{cases}\cos \alpha u(I), & \text{if } u(I)>0,\\ 0, & \text{if } u(I)\leqslant 0.\end{cases}$$

Adaptation of primary detectors: Let adaptive stimulus S_{I_a}, which excites primary detectors to level (2.11) be delivered to the input of the system. Quantities (2.11) are components of excitation vector $\mathcal{F}(I_a)$ generated by stimulus S_{I_a}. Under the influence of prolonged excitation, the sensitivity of primary detectors diminishes proportionally to the level of their excitation by the adaptive stimulus. As a result, stimulus S_I delivered right after the adaptive one generates the following excitation vector:

$$\overline{\mathbf{F}}(I/I_a)=\overline{\mathcal{A}}(I_a, t)\overline{\mathcal{T}}(I), \tag{2.12}$$

where $\mathcal{A}(I_a, t)$ is the adaption operator (Appendix I) and t is the time of delivery of the adaptive stimulus.

Knowing the corresponding excitation vectors (2.12) and zero vector of "gray proper," one can calculate the angle between them:

$$\psi(I)=[\overline{\mathcal{T}}(I=0), \overline{\mathbf{F}}(I/I_a)]. \tag{2.13}$$

Overall level of activity of intensity analyzer. We shall call the sum of activity of all secondary detectors the overall level of analyzer activity.

The excitation profile on the set of secondary detectors (see Appendix 1) is described by the function cos $[f(I) - f(I_j)]$, where I_j is the intensity of the optimum stimulus for the jth detector. In this case, overall activity of all detectors will be:

$$S(I)=\int\limits_0^{\pi/2}\cos[f(I)-f(I_j)]\,df(I_j),$$

i.e.,

$$S(I)=\cos f(I)+\sin f(I). \tag{2.14}$$

Expression (2.14) assumes a maximum value when cos $f(I)$ = sin $f(I)$, i.e., when the components of the excitation vector equal one another. Thus, total illumination of the entire retina from zero to a certain intensity I first leads to an increase in overall analyzer activity, which reaches a maximum with intensities that generate an excitation vector with $\phi = 45°$, after which further increase in intensity leads to decrease in overall analyzer activity.

Overall activity of primary detectors behaves analogously: $S_p(I) = \cos f(I) + \sin f(I)$. With increase in stimulus intensity $S_p(I)$ increases, reaching a maximum at the point where $\cos f(I) = \sin f(I)$, and further increase in intensity leads to decrease in $S_p(I)$.

An analogous function of intensity was described in a study of the magnitude of evoked potential or mean level of activity derived from the optic nerve [18].

In the foregoing, photosensitive elements with characteristics of the (2.3) and (2.4) types were used as photoreceptors. However, the dynamic range of such characteristics does not exceed two logarithmic units. We obtain even closer coincidence of the model's characteristics with the analogous ones of man if we use as photoreceptors elements with characteristics of the following appearance:

$$r(I) = R_{\max} \frac{I^n}{I^n + \sigma^n}, \tag{2.15}$$

where $R_{\max}$ is the maximum response of the receptor, σ is intensity of light at which the response of photoreceptors equals half its maximum value and n is a constant that determines the steepness of responses. For example, with $n = 0.5$, the range over which Weber's ratio is constant, $\Delta I/I = \text{const}$, equals about four logarithmic units, while the indicator of the law of Stevenson is about 0.4. Expression (2.15) describes receptor responses better than a hyperbolic tangent.

APPENDIX 3. COLOR ANALYZER

Sensitivity characteristics of cones and primary color detectors. Color perception is possible only when there is sufficient illumination, when the outside world is perceived by the cones. In twilight conditions, when only the rods are functional, man cannot perceive colors, and the world around him is perceived as being black and white.

There are three types of cones, R, G and B. If the sensitivity characteristics of cones were to be described as functions of frequency of monochromatic radiation, these characteristics would have the same appearance for all three types of cones, although their characteristics are shifted in relation to one another. The general characteristic thus obtained coincides, with accuracy to a constant factor, with the so-called Dartnall nomogram [34].

Hereafter, it is assumed that the cone characteristics are Dartnall functions.

The question arises: Are Dartnall functions optimal from the standpoint of integral sensitivity of the entire analyzer? For this, let us rewrite functional

$$\eta(f_i)=\int_{\varphi_0}^{\varphi_l}\cos\,[\mathbf{F}(f_i(\varphi)),\ \mathbf{F}(f_i(\varphi+\tau))]\,d\varphi \qquad (3.1)$$

(to determine the cosin, see Appendix 1, expression 1.2), using smallness τ, i.e., $f_i(\phi+\tau) = f_i(\phi) + \tau f_i'(\phi)$, in a somewhat different form:

$$\eta(f_i(\varphi))=\int_{\varphi_0}^{\varphi_l}\cos\,(\mathbf{F}(f_i(\varphi)),\ [\mathbf{F}(f_i(\varphi))+\tau F'_\varphi(f_i(\varphi))])\,d\varphi, \qquad (3.2)$$

where F' is a vector with components of the $\{df_i(\phi)/d\phi\}$ type.

Functional (3.2) does not overtly contain variable d. Consequently, for Dartnall functions $\{f_i(\phi)\}$, i = 1, 2, 3, to describe the extremal, the corresponding Hamiltonian [104] along these extremal must be constant:

$$H=-\Phi+\sum_i \Phi_{f_i} f_i=\text{const}, \qquad (3.3)$$

where Φ is a subintegral function of expression (3.2) and Φ_{fi} is its partial derivative $\partial\Phi/\partial f_i'$.

In determining functional (3.2), it must be borne in mind that Dartnall functions are not orthogonal. Condition (3.3) with symmetrical position of Dartnall functions on the frequency axis was directly checked in [103, 106]. It was found that condition (3.3) is satisfied over the entire range of the visible spectrum.

Thus, there are grounds to maintain that Dartnall functions are close to optimal.

However, it is not desirable to make direct use of cones with Dartnall functions of sensitivity as primary detectors determining the components of the color excitation vector. The fact of the matter is that, in this case, the subjective distance between colors would be small and the excitation vector would not exceed the range of one octant.

For this reason, detectors whose responses were obtained as a linear combination of responses of individual cones are used as primary detectors. Also, the direction of the excitation vector should change as much as possible with change in spectral composition of illumination. In the ideal case, the sensitivity characteristics of primary detectors should be described by the corresponding directing cosine curves.

Let us now consider the construction of secondary detectors, without determining the characteristics of primary detectors. As we know, the reaction of the jth secondary detector can be found from the expression

$$d(j,\ \varphi)=(\mathbf{C}_j,\ \mathbf{F}(\varphi)). \tag{3.4}$$

Let us now stipulate that, with frequency of light radiation $\phi = \phi_j$, the jth detector is excited more than any other detector. This condition is met if, at a given value of $\phi=\phi_j$, the reaction of the jth detector reaches a maximum, and the maximum reaction of any detector equals a certain constant value B. In other words,

$$\left.\frac{\partial d(j,\ \varphi)}{\partial\varphi}\right|_{\varphi=\varphi_j}=\left.\left(\mathbf{C}_j,\ \frac{\partial \mathbf{F}(\varphi)}{\partial\varphi}\right)\right|_{\varphi=\varphi_j}=0 \tag{3.5}$$

provided that (3.6)

$$d(j,\ \varphi_j)=B,$$

where $j = 1, \ldots, m$.

In this case, let us first consider condition (3.5), and use (3.6) to find unknown constants that determine the modulus of communication vector. From (3.5) we get

$$\left.\frac{\partial d(j,\ \varphi)}{\partial\varphi}\right|_{\varphi=\varphi_j}=|\mathbf{C}_j|\left|\frac{\partial \mathbf{F}(\varphi)}{\partial\varphi}\right|\cos\left.\left[\mathbf{C}_j,\ \frac{\partial \mathbf{F}(\varphi)}{\partial\varphi}\right]\right|_{\varphi=\varphi_j}=0, \tag{3.7}$$

i.e.,

$$\mathbf{C}_j\perp\left.\frac{\partial \mathbf{F}(\varphi)}{\partial\varphi}\right|_{\varphi=\varphi_j}.$$

Communication vector C_j must be orthogonal to vector $\partial F(\phi)|\partial\phi|\phi = \phi_j$, tangential to spatial curve $\{f_k(\phi)\}$, $k = 1, 2, 3$, and $\phi \in L$ is the interval of frequencies of visible monochromatic radiation. The sought vector C_j is in a plane that is orthogonal to vector $\partial F(\phi)|\partial\phi|\phi = \phi_j$. There may be many such vectors. Let us choose one of them so that the angle between it and excitation vector $F(\phi_j)$ would be as small as possible. To find such a vector, let us project on the plane of communication vectors $\{C_j\}$ excitation vector $F(\phi_j)$ and we shall get vector $F_C(\phi_j)$. Sought vector C_j coincides in direction with vector $F_C(\phi_j)$, i.e.,

$$C_j = \gamma F_C(\varphi_j), \tag{3.8}$$

where γ is a certain constant.

In view of the fact that vector $F'_\phi(\phi)$ is orthogonal to vector $F_C(\phi_j)$--projection of vector $F(\phi_j)$ on the plane of communication vectors $\{C_j\}$, we can submit vector $F(\phi_j)$ as the following sum:

$$F(\varphi_j) = F_C(\varphi_j) + \beta F'_\varphi(\varphi)|_{\varphi=\varphi_j}$$

or

$$F_C(\varphi_j) = F(\varphi_j) - \beta F'_\varphi(\varphi)|_{\varphi=\varphi_j}, \tag{3.9}$$

where β is a certain constant.

Since vector $F_C(\phi_j)$ is orthogonal to vector $F'_\phi(\phi)|_{\phi=\phi_j}$, with consideration of (3.9) we get:

$$(F_C(\varphi_j),\ F'_\varphi(\varphi))|_{\varphi=\varphi_j} = (F(\varphi_j),\ F'_\varphi(\varphi))|_{\varphi=\varphi_j} - \\ - \beta\,|F'_\varphi(\varphi)|^2_{\varphi=\varphi_j} = 0$$

or

$$\beta = \frac{(F(\varphi),\ F'_\varphi(\varphi))}{(F'_\varphi(\varphi),\ F'_\varphi(\varphi))}\bigg|_{\varphi=\varphi_j}. \tag{3.10}$$

Moreover, considering condition (3.6), we can obtain the value of the other unknown constant:

$$\gamma = \frac{B}{(F(\varphi),\ F(\varphi)) - \beta\,(F'_\varphi(\varphi),\ F(\varphi))}\bigg|_{\varphi=\varphi_j}. \tag{3.11}$$

Knowing curve $\{f_k(\phi)\}$, ($\phi \in L$, $k = 1, 2, 3$), we can calculate communication vector C_j (3.8), where coefficients γ and β can be found from conditions (3.10) and (3.11). The communication vector enables us to calculate the characteristics of output detectors (3.4). Figure 40 illustrates the respones of different output detectors calculated by the method described in [105]. If we were to choose any three independent orthogonal functions out of the existing set of responses, these functions could be used as the characteristics of primary detectors.

Two-dimensional invariant spaces of color adaptation operator. Let a certain adaptive stimulus S_{ϕ_0} be given, to which corresponds excitation vector $F(\phi_0)$ with components $\{f_i(\phi_0)\}$. Let the vector be transformed under the influence of prolonged viewing of stimulus S_{ϕ_0} as follows:

$$F(\varphi_0/\varphi_0) = \mathcal{A}(\varphi_0,\ t)\,F(\varphi_0), \tag{3.12}$$

where $\mathcal{A}(\phi_0, t)$ is the adaptation operator. $\mathcal{A}(\phi_0, t)$ is a diagonal operator, with the following coefficients on the main diagonal:

$$a_{ii} = 1 - \gamma(t)\,|f_i(\varphi)|. \tag{3.13}$$

In the general case, vector $F(\phi_0/\phi_0)$ is not collinear to vector $F(\phi_0)$. The question arises: In what cases is the trajectory of the vector flat in the course of adaptation and, in addition, does it contain the vector of white color? In other words, in what cases does adaptation have no effect on the perceived color of the stimulus?

Let there be the three following vectors: purely monochromatic vector in the absence of adaptation $F(\phi)$, white vector $F(\delta)$ with components $f_i(\delta)$ and vector $\partial F(\phi_0/\phi_0)\ \partial t$, tangential to the trajectory of adaptation. The components of the last vector equal $\gamma'(t)$, $\{f_j^2(\phi_0)\}$, $j = 1, 2, 3$. If all these vectors are in the same plane at any point in time t, the trajectory of vector $F(\phi_0/\phi_0)$ will be flat. In this case, all three vectors should be linked with a linear function. Then the determinant plotted on these vectors should equal 0:

$$\Delta(f_1, f_2, f_3) = -\gamma'(t) f(\delta) \begin{vmatrix} 1 & 1 & 1 \\ f_1(\varphi_0) & f_2(\varphi_0) & f_3(\varphi_0) \\ f_1^2(\varphi_0) & f_2^2(\varphi_0) & f_3^2(\varphi_0) \end{vmatrix} = 0. \qquad (3.14)$$

Since we are dealing with an alternant [Vandermond determinant], condition (3.14) can be replaced with condition:

$$(f_1-f_2)(f_1-f_3)(f_2-f_3)=0. \qquad (3.15)$$

Thus, for the stimulus not to change its chromaticity during adaptation, this stimulus must excite to an equal extent at least two of the three primary detectors.

APPENDIX 4. LINE SLANT ANALYZER

Primary detectors of line slant. Distinction of areas with illumination gradient: Distinction of the range of illumination by means of on or off receptive fields has a substantial flaw: in order to distinguish a black line on a white background and white line on a black background, different systems of receptive fields must be used: off-on in the first case and on-off in the second. Such a system is cumbersome and unreliable.

Let us consider another method that is suitable for distinguishing both a white outline on a black background and a black outline on white. Figure 74 illustrates a system that will function only if its receptor layer makes small random jumps all of the time. Let the image of a black-white border be projected on the receptive field. Two groups of receptors can be distinguished. On some receptors, the level of illumination changes constantly since the range of change in illuminations shifts from one receptor to another in the presence of random tremor. The illumination level remains constant on the rest of the receptors. As a result, a variable signal arises at the output of the first group of receptors and a constant one at the output of the second group of receptors. The signal passes from the receptor to the input of the underlying neuron via the excitation and inhibition channel. Transmission of the signal via the inhibitory channel lags in relation to the excitatory channel.

When there is an unchanging image on the retina, signals from the constantly illuminated group of receptors passing via the inhibitory and excitatory channels compensate one another. As a result, the output signal of these neurons is found to equal zero soon after turning the stimulus on. If the signal at the output of the receptors changes in time, excitation and inhibition passing to the input of the second neuron are unable to compensate one another. As a result, this signal passes only from the receptors, on which the limit of illumination is projected in the presence of tremor. This method makes it possible to single out a white outline on a black background and a black outline on a white background.

This method can also be well-used in the visual analyzer, since the eye has the required random tremor. Thus, frequency of tremor in man constitutes 150 Hz and amplitude is about 18 s of the visual angle, which corresponds to shifting of an image in the central part of the retina within the range of 1-3 cones [11]. Interaction between bipolar, amacrine and ganglion cells may be responsible for distinction of the variable component, generating phasic reactions in ganglion cells [22].

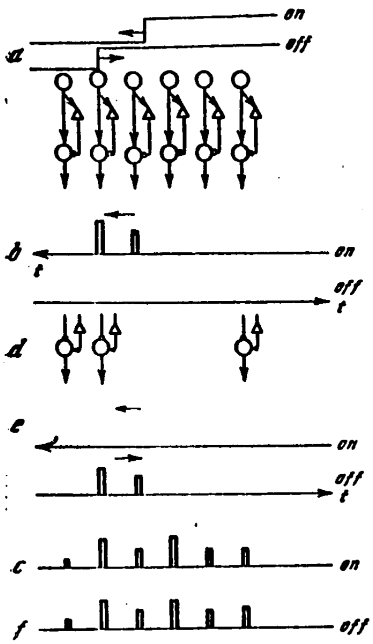

Figure 74.
Distinguishing outline of an image by menas of tremor

In the following, it is assumed that to construct primary detectors of orientation use is made of signals taken from neurons, on which there is preliminary distinction of image outline.

Organization of receptive field of primary detectors: Let a segment of image outline be projected in the receptive field of a local analyzer. Under the influence of light at the output of receptors or neurons distinguishing the outline, there is appearance of signal $r_i(\mathrm{I})$, $i = 1, \ldots, s$, where i is receptor number, s is the number of photoelements in the receptive field and I is intensity of receptor illumination. The set of signals $\{r_i(\mathrm{I})\}(i = 1, \ldots, s)$ is a discrete approximation of the image delivered to the receptive field of the local image analyzer. We shall consider set $\{r_i(\mathrm{I})\}$ $(i = 1, \ldots, s)$ as components of s-dimensional vector $\mathcal{R}$. The orientation of a local line segment is given by the number ϕ (angle of tilt in a given system of coordinates), which takes on any value in the interval $[0, \pi]$. It is assumed that the value of the parameter is coded unambiguously by the direction of excitation vector $F(\phi)$ or number $\psi \in [0, 2\pi]$.

Vector $F(\phi)$ must be at least two-dimensional, and hereafter we assume that dimensionality equals two. Consequently, we must have two independent primary detectors whose responses are described by the functions:

$$f_2(\varphi) = \sin 2\varphi \quad \text{и} \quad f_1(\varphi) = \cos 2\varphi. \tag{4.1}$$

Thus, the image on the retina generates s-dimensional vector $\mathcal{R}$. Then, by means of a certain degenerate operator $\mathcal{B}_1$, vector $\mathcal{R}$ is transformed into the second excitation vector $\mathcal{F}(\phi)$. The appearance of operator $\mathcal{B}_1(\mathcal{R} \xRightarrow{\mathcal{B}_1} \mathcal{F}(\phi))$ is determined by the contacts between receptors and primary detectors. Apparently, there are many [or a set] such transformations, with which the following equation applies:

We shall discuss below two methods of determining operator $\mathcal{B}_1$: Let the receptive field of primary detectors be divided into two intersecting connected zones. We shall call the zone, illumination of which elicits inhibition of a primary detector, the inhibitory zone, and the one illumination of which excites the primary detector, the excitatory zone. Let the influence of each point of the illuminated receptive field on detector activity be constant and independent of the position of the point in the receptive field. The projection of the line on the receptive field elicits a reaction by the primary detector, formed by the sum of signals from the inhibitory R_T and excitatory R_B areas. These signals equal the cosine and sine of the dual angle of inclination of line ϕ. In order to determine the form of receptive field of the corresponding primary detector, let us transform (4.1) into the following expressions:

$$f_2(\varphi) = \sin 2\varphi = \cos^2(\varphi + 45°) - \sin^2(\varphi + 45°), \tag{4.2}$$

$$f_1(\varphi) = \cos 2\varphi = \cos^2\varphi - \sin^2\varphi. \tag{4.3}$$

Thus, according to (4.2) and (4.3), the overall signal from excitatory regions should equal $\cos^2\phi$ and $\cos^2(\phi+45°)$ and the inhibitory one should equal $\sin^2\phi$ and $\sin^2(\phi+45°)$, respectively. Consequently, the length of the presented line lying in the excited part of the receptive field is $\rho_B = \cos^2\phi$ or $\cos^2(\phi+45°)$, and for the line segment in the inhibitory zone, $\sin^2\phi$ or $\sin^2(\phi+45°)$. The overall length of the vector-radius for the entire receptive field is $\sin^2\phi + \cos^2\phi = 1$. Thus, the vector-radius of the receptive field is constant--the receptive field is in the form of a circle.

The flaw of such organization of the receptive field is that, in this case, the reaction of primary detectors depends on the presence of noise contained in the image. Indeed, let the receptive field of the analyzer be illuminated by random spots. The spots are small, but their density is rather high. If the density of noise is high enough, the overall output signal of the primary detector from both zones of the receptive field separately is proportional to the area of these regions. The area of the excitatory region in the previously proposed case is:

$$S_B = \frac{1}{2}\int_0^{2\pi} \rho^2 d\varphi = \frac{1}{2}\int_0^{2\pi} \cos^4\varphi d\varphi = \\ = \frac{3}{16}\varphi\Big|_0^{2\pi} + \frac{1}{8}\sin 2\varphi\Big|_0^{2\pi} + \frac{1}{64}\sin 4\varphi\Big|_0^{2\pi} = \frac{3}{8}\pi. \tag{4.4}$$

The area of the inhibitory region is found as the difference between areas of the circle and excitatory region, i.e.,

$$S_T = \pi - \frac{3}{8}\pi = \frac{5}{8}\pi. \tag{4.5}$$

From these results we see that with noisy illumination of the receptive field the signal at the output of primary detectors does not equal zero:

$$f_1(\varphi) = S_B - S_T = -\pi/4, \qquad f_2(\varphi) = S_B - S_T = -\pi/4, \tag{4.6}$$

which is equivalent to excitation vector $\mathcal{F}(\phi = 112°30')$ with equal negative components. Thus, in the presence at the input of only noisy illumination, there is the illusion of perception of a line tilted at 112°30'.

In order to eliminate this flaw, let us consider a different structure of organization of the primary detector receptive field.

Each point on the receptive field has the same effect on activity of a primary detector. When an outline is projected in the detector's receptive field, the absolute value of its reaction equals the length of the line in the receptive field.

The overall reaction of the primary detector should equal $f_1(\phi) = \sin 2\phi$ and $f_2(\phi) = \cos 2\phi$, respectively. Consequently, the receptive field in polar coordinates has the following appearance:

$$\rho_1(\varphi) = |\sin 2\varphi| \quad \text{и} \quad \rho_2(\varphi) = |\cos 2\varphi|. \tag{4.7}$$

Figure 49 illustrates the form of receptive field thus obtained. In constructing a primary detector, it must be borne in mind that a "plus" refers to regions that have an excitatory effect on the activity of the primary detector and "minus" to those that have an inhibitory effect.

With such organization of the receptive field, the reaction of primary detectors does not depend on presence of random uniform noise in illumination. Indeed, in this case the areas of the inhibitory and excitatory zones are equal, so that the signals from both zones balance one another.

Finally, there can also be a third form of receptive field. Let there be a center given in the receptive field, through which a line is drawn. The tilt of this line equals zero. The orientation of the arbitrary line is determined by angle ϕ, which it forms with the line that has zero tilt. The magnitude of contact between the receptor and primary detector is proportional to $\cos 2\phi$ (or $\sin 2\phi$).

Mixture effects in orientation analyzer: Let there be two centered lines, L_{ϕ_1} and L_{ϕ_2}, projected on the receptive field, which correspond to excitation vectors:

$$\mathcal{F}(\varphi_1) = (\cos 2\varphi_1,\ \sin 2\varphi_1) \quad \text{и} \quad \mathcal{F}(\varphi_2) = (\cos 2\varphi_2,\ \sin 2\varphi_2). \tag{4.8}$$

As a result of joint excitation of primary detectors, their excitation level is:

$$\begin{aligned} f_2(\varphi_1, \varphi_2) &= \sin 2\varphi_1 + \sin 2\varphi_2 = 2\sin(\varphi_1 + \varphi_2)\cos(\varphi_1 - \varphi_2), \\ f_1(\varphi_1, \varphi_2) &= 2\cos(\varphi_1 + \varphi_2)\cos(\varphi_1 - \varphi_2). \end{aligned} \tag{4.9}$$

The vector with components (4.9) corresponds in direction with the excitation vector generated by line tilt $(\phi_1+\phi_2)/2$. Thus, with simultaneous delivery to the receptive field of two lines, there is generation of a vector that corresponds to a line, which is the bissectrix of the small angle between these lines.

Adaptation effects in orientation analyzer. Normalization effect: During prolonged viewing of a line, its slant does not change when this line corresponds to one of the eigen vectors of the adaptation operator, i.e., the vector in which either all non-zero components equal one another, or else only one component does not equal zero (Appendix 1). The former case corresponds to lines with tilt:

$$\varphi_k = k\pi/8, \quad (k = 1,\ 3,\ 5,\ 7), \tag{4.10}$$

and the latter, with tilt:

$$\varphi_k = k\pi/8, \quad (k = 0,\ 2,\ 4,\ 6). \tag{4.11}$$

Let us consider the adaptation properties under the influence of lines with tilts of the (4.10) and (4.11) type. For this, let us determine how the angle between the arbitrary line and closest line with tilt (4.11) changes with adaptation, i.e.,

$$\frac{\partial}{\partial t}\cos\left[\mathrm{F}(\varphi/\varphi),\ \mathcal{F}(\varphi_k)\right]=\frac{\partial}{\partial t}\,\frac{\Sigma\,(1-\gamma(t)\,|f_i(\varphi)|)\,f_i(\varphi_k)\,f_i(\varphi)}{[\Sigma\,(1-\gamma(t)\,|f_i(\varphi)|)^2 f_i^2(\varphi)]^{1/2}}$$

Putting $a_i=1-\gamma(t)|f_i(\varphi)|$, we have

$$\delta(t)=\frac{\partial}{\partial t}\cos\left[\mathrm{F}(\varphi/\varphi),\ \mathcal{F}(\varphi_k)\right]=\frac{\partial}{\partial t}\,\frac{\Sigma a_i f_i(\varphi_k)\,f_i(\varphi)}{[\Sigma a_i^2 f_i^2(\varphi)]^{1/2}}. \tag{4.12}$$

Let $\varphi_k=0$ or $\varphi_k=\pi/2$,

$$f_1(\varphi_k)=\cos 2\varphi_k=\pm 1 \quad \text{и} \quad f_2(\varphi_k)=\sin 2\varphi_k=0. \tag{4.13}$$

Considering (4.13), expression (4.12) assumes the following appearance:

$$\begin{aligned}\delta(t)&=\frac{\partial}{\partial t}\,\frac{a_1 f_1(\varphi)}{[\Sigma a_i^2 f_i^2(\varphi)]^{1/2}}\,f_1(\varphi_k)=\\&=\frac{a_1' f_1(\varphi)\,\Sigma a_i^2 f_i^2-a_1 f_1 \Sigma a_i a_i' f_i^2}{[\Sigma a_i^2 f_i^2]^{3/2}}\,f_1(\varphi_k).\end{aligned} \tag{4.14}$$

Since the denominator of (4.14) is positive, the sign of the entire expression is determined by the sign of the numerator. After reducing in the numerator $\delta_1(t)$ we have

$$\delta_1(t)=a_2 f_2^2[a_1' a_2-a_1 a_2']\,f_1(\varphi)\,f_1(\varphi_k). \tag{4.15}$$

Since $a_2>0$, $a_2 f_2^2>0$ also, and the sign of (4.15) is determined by the sign of the expression:

$$\delta_2(t)=(a_1' a_2-a_1 a_2')\,f_1(\varphi)\,f_1(\varphi_k). \tag{4.16}$$

After substituting in (4.16) the values $a_i = 1 - \gamma(t)\,|f_i(\phi)|$ and $a_i' = -\gamma'(t)\,|f_i(\phi)|$ we get

$$\delta_3(t)=f_1(\varphi)\,f_1(\varphi_k)\,(|f_2(\varphi)|-|f_1(\varphi)|)\,\gamma'(t). \tag{4.17}$$

Since $\gamma'(t)>0$, the sign is determined by the sign of

$$\delta_4(t)=f_1(\varphi)\,f_1(\varphi_k)\,(|f_2(\varphi)|-|f_1(\varphi)|). \tag{4.18}$$

Let us first consider the case $\phi_k = 0$, i.e., $f_1(\phi_k) = 1$ in the interval of $0<\phi<45°$, $f_1(\phi)>0$ and $f_1(\phi)>f_2(\phi)$. Thus, with $\phi\in[0, 45°]$, expression (4.18) is negative. In other words, during adaptation the angle of $\mathrm{F}(\phi/\phi)$, $\mathcal{F}(\phi_k)$, ($\phi_k = 0$; $0<\phi<45°$) increases (cosine decreases). In the interval of $\phi\in(-45°, 0)$ with $\phi_k = 0$, expression (4.18) is also negative, i.e., this angle also increases during adaptation. Indeed, if $0>\phi>-45°$, then $|f_1(\phi)|>|f_2(\phi)|$, $f_1(\phi)>0$, $f_1(\phi_k) = 1$, consequently $\delta_4(t)<0$.

In the case where $\phi_k = \pi/2$, $f_1(\phi_k) = -1$. Let $\phi\in(67°30', 112°30')$ and $\phi\neq 90°$. Then $f_1(\phi)<0$ and $f_1(\phi)f_1(\phi_k)>0$. Moreover, $|f_1(\phi)|>|f_2(\phi)|$ and, consequently, $\delta_4(t)<0$.

Let $\phi_k = 2\pi/8$ or $\phi_k = 6\pi/8$, i.e., $f_1(\phi_k) = \cos 2\phi_k = 0$ and $f_2(\phi_k) = \sin 2\phi_k = \pm 1$. In this case, pursuing the analogous reasoning as in the first case, the sign of derivative $d\cos[\mathrm{F}(\phi/\phi), \mathcal{F}(\phi_k)])/dt$ is determined by the sign of the expression:

$$\delta_4'(t)=f_2(\varphi)\,f_2(\varphi_k)\,[|f_1(\varphi)|-|f_2(\varphi)|]. \tag{4.19}$$

Let us consider the case where $\phi_k = 2\pi/8$ and $f_2(\phi_k) = 1$. In addition, $\phi \in (22°30', 67°30')$ and $\phi \neq 2\pi/8$. In this case, $f_2(\phi)>0$, $|f_2(\phi)|>|f_1(\phi)|$ and, consequently, expression (4.19) is negative.

Let then $\phi_k = 135°$ ($f_2(\phi_k) = -1$), $\phi \in (112°30', 157°30')$ and $\phi = 135°$, i.e., $f_2(\phi)<0$, $f_2(\phi_k)<0$ and $f_2(\phi)f_2(\phi_k)>0$. Since in this interval $|f_2(\phi)|>|f_1(\phi)|$, again $\delta_4'(t)<0$.

During prolonged viewing of a line with arbitrary tilt, the angle between the vector corresponding to this line and the closest eigen vector $\mathcal{F}(\phi_k)$, where $\phi_k = k\pi/8$, ($k = 0, 2, 4, 6$) increases continuously. Lines with arbitrary tilt that is other than the tilts that generate eigen vectors (4.10) and (4.11) alter their slant in the course of adaptation, coming close to one of the nearest lines with tilts (4.10). The slightest deviation of the lines from slants (4.11) leads to perception thereof as oriented in the direction of one of the nearest lines (4.10). Hereafter, we shall call lines (4.11) unstable eigen lines, and those with tilts (4.10) stable.

In man, stable eigen lines are the vertical or horizontal in the gravity field. These lines should excite both primary detectors equally. To satisfy this condition, the optimum axes of the detector receptive field should be turned by 22°30' in relation to the coordinate system of the gravity field.

Aftereffect: Let there be two stimuli, vertical line L_{ϕ_0}, which corresponds to vector $\mathcal{F}(\phi_0)$, and arbitrary line L_ϕ with excitation vector $\mathcal{F}(\phi)$. Line L_ϕ is the adaptive line, after which vertical line L_{ϕ_0} is immediately presented. With consideration of adaptation, line L_{ϕ_0} generates a transformed excitation vector:

$$\mathbf{F}(\varphi_0/\varphi) = \mathcal{A}(\varphi, t)\mathcal{F}(\varphi_0), \tag{4.20}$$

where $\mathcal{A}(\phi, t)$ is the adaptation operator and t is the time of delivery of the adaptive stimulus (Appendix 1).

Vector $F(\phi_0/\phi)$ is not collinear with vector $\mathcal{F}(\phi_0)$ in the general case. Let us find the angle of $F(\phi_0/\phi)$, $\mathcal{F}(\phi_0)$ as a function of tilt of the adaptive line. The cosine of the angle between the initial and transformed excitation vectors (4.20) equals:

$$\cos[\mathcal{F}(\varphi_0), \mathbf{F}(\varphi_0/\varphi)] = \\ = \frac{\cos^2 2\varphi_0 (1 - \gamma(t)|\cos 2\varphi|) + \sin^2 2\varphi_0 (1 - \gamma(t)|\sin 2\varphi|)}{[\cos^2 2\varphi_0 (1 - \gamma(t)|\cos 2\varphi|)^2 + \sin^2 2\varphi_0 (1 - \gamma(t)|\sin 2\varphi|)^2]^{1/2}}. \tag{4.21}$$

If the tilt of the vertical in the coordinate system of primary detectors equals 22°30', expression (4.21) acquires the following appearance:

$$\cos[\mathcal{F}(\varphi_0), \mathbf{F}(\varphi_0/\varphi)] = \frac{\sqrt{2}}{2} \times \\ \times \frac{2 - \gamma(t)(|\cos 2\varphi| + |\sin 2\varphi|)}{[(1 - \gamma(t)|\cos 2\varphi|)^2 + (1 - \gamma(t)|\sin 2\varphi|)^2]^{1/2}}. \tag{4.22}$$

Expression (4.22) equals 1 with $\phi = r\pi/8$, $r = 1, 3, 5, 7$. In other words, with the given values of the adaptive stimulus, the angle between vectors $F(\phi_0/\phi)$ and $\mathcal{F}(\phi_0)$ does not change; consequently, adaptation, which develops to the same extent in both primary detectors, does not affect perception of tilt of the vertical line.

The value of cosine (4.22) enables us to determine the angle by which the vertical should be turned so that it is subjectively perceived again as a vertical after adaptation--the angle equals half the angle of arc cos $[\mathcal{F}(\phi_0), F(\phi_0/\phi)]$.

Simultaneous contrast. Description of "simultaneous contrast" interaction: When there is inhibitory interaction between homonymous detectors of spatially different analyzers, one can calculate the subjective change in angle between two lines using the following formula:

$$\Delta\psi = \frac{1}{2}\left\{\arccos\left[\frac{(1+\alpha^2)\cos\Delta\varphi - 2\alpha}{1+\alpha^2-2\alpha\cos\Delta\varphi}\right] - \Delta\varphi\right\}, \tag{4.23}$$

where α is the coefficient of interaction $0 \leqslant \alpha \leqslant 1$; $\Delta\phi$ is the angle between excitation vectors corresponding to interacting lines (Appendix 1).

In the general case, coefficient α depends on the distance between interacting primary detectors of different local analyzers. Figure 56b illustrates the function of quantity $1/2\psi(\Delta\phi) = f(\Delta\phi)$--characteristic of "simultaneous contrast." It was considered that $\alpha(\Delta\phi) = \alpha_0 e^{-\beta \sin \Delta\phi/2}$, where α_0 and β are constants. The calculations were made for different values of constants α_0 and β.

Figure 57b shows the effect of an inductive line on the reaction elicited by the optimum line in the main test field of primary detectors of orientation. In the calculations, it was also assumed that the coefficient of interaction is a function of angle $\Delta\phi$. It was considered that $\alpha(\Delta\phi) = \alpha_0 e^{-\beta \sin \Delta\phi/2}$.

Poggendorff illusions: Figure 59 illustrates the objective location of lines (solid lines) and their subjective (dotted line) position with Poggendorff's illusion. The distance between lines 1-1 and 2-2 equals d. Lines a-a and b-b form angle ϕ with lines 1-1 and 2-2. Then the segment $AA_2 = d \operatorname{ctg} \phi$, and $CA_2 = d \operatorname{ctg} (\phi + \Delta\psi)$, where $\Delta\psi$ is the subjective increase in angle ϕ during interaction of the lines (see (4.23)). In turn, the sought subjective shift Δb equals $\Delta b = AA_2 - CA_2$, i.e.,

$$\Delta b = \frac{\sin\Delta\psi}{\sin\varphi \sin(\varphi + \Delta\psi)} d. \tag{4.24}$$

Masking effect: In this section there is discussion of the effect of inertia of inhibitory contacts that implement "simultaneous contrast" interaction on the duration of excitation of the orientation detector by the test line in excess of a certain threshold level θ.

It was assumed that the inertia of connections involved in "simultaneous contrast" could be reduced to inertia of primary detectors. Let the transient process, which arises in primary detectors upon use of the stimulus, be described by the expression:

$$f_i^0(\varphi, t) = f_i(\varphi)(1 - e^{-\beta_1 t})[1 - h(t - t_0)], \tag{4.25}$$

and with stimulus off:

$$f_i(\varphi, t) = f_i^0(\varphi, t) e^{-\beta_2 (t - t_0)} h(t - t_0), \tag{4.26}$$

where β_1 and β_2 are time constants of build-up and extinction, respectively, of excitation of primary detectors, and usually $\beta_1 > \beta_2$ [108, 109]; $f_i(\phi, t)$ is the output signal of the ith primary detector at time t; $h(t-t_0)$ is a Heaviside function:

$$h(t-t_0)=\begin{cases}0, & \text{if } t\leqslant t_0,\\ 1, & \text{if } t>t_0.\end{cases} \tag{4.27}$$

Thus, expressions (4.25) and (4.26) describe the level of detector excitation after discontinuing the stimulus at time t_0.

Let us consider the case of backward masking described by Sekular [102]. In this case, vertical line L_{ϕ_0} served as the test stimulus, while L_ϕ with arbitrary tilt ϕ served as the masking one. There was a constant interval, $\tau_1 = 40$ ms, between the time of discontinuing the test line and delivering the masking one. The masking stimulus delivery time was constant, with $\tau_2 = 100$ ms, while the duration of test stimulus τ_0 could be changed during the experiment.

How long should test stimulus L_{ϕ_0} last so that its detector would be excited for a time t_{cr} in excess of threshold level θ? We can find the components of the excitation vector after discontinuing the test stimulus, with consideration of inertia, using the expression:

$$\mathbf{F}(\varphi_0,\ t)=(\cos 2\varphi_0,\ \sin 2\varphi_0)(1-e^{-\beta_1\tau_0})\,h(t-\tau_0)\,e^{-\beta_2(t-\tau_0)}. \tag{4.28}$$

For the masking stimulus, the excitation vector acquires the following appearance:

$$\mathbf{F}(\varphi,\ t)= \\ =\begin{cases}(\cos 2\varphi,\ \sin 2\varphi)(1-e^{-\beta_1(t-\tau_0-\tau_1)}), & \text{if} \quad \Delta\geqslant t>\tau_0+\tau_1,\\ (\cos 2\varphi,\ \sin 2\varphi)(1-e^{-\beta_1\tau_1})e^{-\beta_2(t-\Delta)}, & \text{if} \quad t>\Delta,\end{cases} \quad (4.29) \tag{4.29}$$

where $\Delta = \tau_0 + \tau_1 + \tau_2$, and time t is clocked from the moment of delivery of the test stimulus.

The components of vectors $F(\phi_0,\ t)$ and $F(\phi,\ t)$ describe the state of primary detectors of different local analyzers of orientation. With consideration of inhibition, which produces "simultaneous contrast," instead of vectors $F(\phi_0,\ t)$ and $F(\phi,\ t)$, we must consider the following vectors:

$$\mathbf{F}'(\varphi_0,\ t)=\mathbf{F}(\varphi_0,\ t)-\alpha\mathbf{F}(\varphi,\ t) \text{ and } \mathbf{F}'(\varphi,\ t)=\mathbf{F}(\varphi,\ t)-\alpha\mathbf{F}(\varphi_0,\ t). \tag{4.30}$$

Knowing the resultant vector $F'(\phi_0,\ t)$, we can determine the level of excitation of the output detector for the ϕ_0th tilt of the line:

$$d(j,\ \varphi_0)=(\mathbf{C}_j,\ \mathbf{F}'(\varphi_0,\ t))=(\mathbf{C}_j,\ \mathbf{F}(\varphi_0,\ t)-\alpha\mathbf{F}(\varphi,\ t)). \tag{4.31}$$

Considering (4.28) and (4.29), from (4.31) we obtain the following after performing the most elementary operations:

$$d(j,\ \varphi)=R^2(1-e^{-\beta_1\tau_0})e^{-\beta_2(t-\tau_0)}-\alpha R^2\cos 2\Delta\varphi H(t), \tag{4.32}$$

where $R^2=|\mathcal{F}(\varphi_0)|^2=1$,

$$H(t)=\begin{cases}1-e^{-\beta_1(t-\tau_0-\tau_1)}, & \text{if} \quad \Delta>t>\tau_0+\tau_1,\\ (1-e^{-\beta_1\tau_1})e^{-\beta_2(t-\Delta)}, & \text{if} \quad t>\Delta=\tau_1+\tau_2+\tau_0,\end{cases} \tag{4.32a}$$

and $\Delta\phi$ is the angle between the test and masking line.

Knowing $d(j,\ \phi,\ t)$ (4.32), let us find a duration of the test stimulus that would satisfy condition $d(j,\ \phi_0,\ t_{cr}) \approx \theta$. Considering (4.37) and that R = 1, we get the following expression:

$$(1 - e^{-\beta_1\tau_0})\, e^{-\beta_2(t_{cr}-\tau_0)} - \alpha \cos 2\Delta\varphi H(t_{cr}) = \theta, \tag{4.33}$$

where $H(t_{cr})$ is determined with expression (4.32a), with $t = t_{cr}$.

With $\theta \approx 0$, the condition will be satisfied if $d(j,\ \phi,\ t)>0$ at the time of discontinuing the masking stimulus. Thus, condition (4.33) can be replaced by another condition: at the time of discontinuation of the masking stimulus, the following inequality must be satisfied:

$$(1 - e^{-\beta_1\tau_0})\, e^{-\beta_2(\tau_1+\tau_2)} - \alpha \cos 2\Delta\varphi (1 - e^{-\beta_1\tau_1}) \geqslant 0$$

or

$$1 - \alpha \cos 2\Delta\varphi (1 - e^{-\beta_1\tau_1})\, e^{\beta_2(\tau_1+\tau_2)} > e^{-\beta_1\tau_0}. \tag{4.34}$$

Taking the logarithm of (4.34), we have

$$\ln [1 - \alpha \cos 2\Delta\varphi (1 - e^{-\beta_1\tau_1})\, e^{\beta_2(\tau_1+\tau_2)}] \geqslant -\beta\tau_0. \tag{4.35}$$

If $\beta_1\tau_2 \ll 1$, i.e.,

$$\ln [1 - \alpha \cos 2\Delta\varphi e^{\beta_2(\tau_1+\tau_2)}] \geqslant -\beta\tau_0, \tag{4.35a}$$

expression (4.35), with consideration of $\alpha \cos 2\ \Delta\phi\ e^{\beta_2(\tau_1+\tau_2)}<1$, can be simplified significantly. By expanding logarithm (4.35a) into a Taylor series and discarding all higher terms of these series, we finally get:

$$\tau_0 = \frac{1}{\beta_1} \alpha \cos 2\Delta\varphi e^{\beta_2(\tau_1+\tau_2)}. \tag{4.36}$$

Figure 62 illustrates a function of the (4.36) type.

Differential sensitivity of the model of a line orientation analyzer. Differential sensitivity is determined by $\Delta\phi^{-1}$, which is the reciprocal of the change in tilt angle ϕ of line L_ϕ at which the subjective distance between compared stimuli equals a threshold value. The subjective threshold distance between stimuli is determined by the angle by which the excitation vector must be turned so that the excitation maximum would shift from a given output detector to the next one. The angle of rotation of the excitation vector depends on the number of secondary detectors that code line tilt: the larger their number, the smaller the needed angle of vector rotation and the shorter the subjective threshold distance between stimuli. For example, with change in line tilt from 0 to 60°, let the excitation vector change its direction from 0 to 120°. To code the direction of an excitation vector that assumes any value from 0 to 120°, there are three secondary detectors. Then, in order to detect changes in direction of the excitation vector it should be turned by at least an angle of 40°, i.e., the slant of the line should be changed by 20°. If, however, there are six secondary detectors, instead of three, intended for coding these inclinations of the excitation vector, the minimal detectable changes constitute 20° (instead of 40° as in the preceding case), which corresponds to a 10° change in line tilt (instead of the 20° in the preceding case). If there are three secondary detectors intended for coding tilts of excitation vectors from 0 to 20° and nine secondary detectors for those from 20 to to 40°, the subjective threshold distances between lines generating excitation vectors will differ, depending on the tilt of the analyzed lines. Thus, the subjective threshold distance for lines with a tilt of 0 to 10° is 3 times greater than the analogous distance for lines with a tilt of 10 to 20°. If the subjective threshold is a constant unrelated to value of the stimulus, differential sensitivity will also be a constant equaling half the angle determining the subjective threshold.

It was experimentally demonstrated, however, that man has greater sensitivity to changes in inclination of vertical or horizontal lines than diagonal ones [109, 111]. This inconsistency between the model and psychophysical data can be eliminated if more secondary detectors are assigned for coding lines that are close to vertical or horizontal than for diagonal lines. There are data to the effect that this is expressly how dissimilar sensitivity of man [110] and animals [73] to changes in tilts of lines with different orientation is provided.

APPENDIX 5. ANALYZER OF DIRECTION AND SPEED OF MOTION

Primary detectors of speed of motion. Let us consider the construction of primary detectors based on ordinary DC cells: slow *on* and fast *on-off* neurons that have responses of the following type:

$$f_1(\varphi, v)=c_1(v)\cos\varphi, \quad f_2(\varphi, v)=c_1(v)\cos(\varphi+120^\circ), \quad f_3(\varphi, v)=c_1(v)\cos(\varphi+240^\circ) \tag{5.1}$$

for the *on* type of cells and

$$f_i(\varphi, v)=c_2(v)\cos(\varphi+\theta_i), \quad \theta_i=0,\ 90,\ 180,\ 270^\circ \tag{5.2}$$

for the *on-off* type of cells (Figure 63), where $c_i(v)$, $(i = 1, 2)$ is a function of velocity of the stimulus.

If we consider that the entire cosine curve response can be realized only if there is spontaneous neuronal activity, (5.1) and (5.2) should be replaced with the following expressions:

$$f'_i(\varphi, v)=c_1(v)[1+\cos(\varphi+\theta_i)], \quad \theta_i=(i-1)\cdot 120^\circ, \quad (i=1, 2, 3) \tag{5.3}$$

and

$$f'_i(\varphi, v)=c_2(v)[1+\cos(\varphi+\theta_i)], \quad \theta_i=(i-1)\cdot 90^\circ, \quad (i=1, 2, 3, 4). \tag{5.4}$$

Let there also be elements that summate the signal from *on* and *on-off* cells separately, i.e.,

$$f_1(v)=c_1(v)\sum^{3} f'_i(\varphi, v)\doteq c_1(v), \tag{5.5}$$

$$f_2(v)=c_2(v)\sum^{4} f_i(\varphi, v)=c_2(v). \tag{5.6}$$

As a result, the responses of the elements do not depend on the direction of movement of the stimulus. Oyster [97] indicates that the function $c_i(v)$, $(i = 1, 2)$ within the range of (*on* or *on-off*) cells is rather constant, particularly for the *on* type of primary detectors of direction of motion.

Functions (5.5) and (5.6) can be viewed as the responses of primary detectors of velocity of a stimulus.

However, functions of the (5.1) and (5.2) type can also be used directly as primary detectors.

Adaptation effects in the analyzer of direction of motion. The primary detectors of the direction analyzer are described by the functions:

$$f_1(\phi) \equiv \cos\phi \quad \text{and} \quad f_2(\phi) \equiv \sin\phi \tag{5.7}$$

Functions (5.7) differ from the functions describing sensitivity of primary detectors of line slant only in that they are extended twice as much on axis ϕ. This means that all functions that are valid for the line orientation analyzer also retain their validity for the analyzer of direction of movement, but for angles that are twice the size of those for line tilt. Consequently, the eigen directions of movement are 0, 45, 90, 135, 180, 225, 270 and 315°, and the stable ones are 45, 135, 225 and 315°. If the optimum axes of primary detectors of direction were to be turned 45°, i.e., function (5.7) modified in the following manner: $f_1(\phi) \equiv \cos(\phi+45°)$ and $f_2(\phi) \equiv \sin(\phi+45°)$, the stable directions would be 0, 90, 180 and 270°. The function analogous to the successive effect of tilt in the tilt analyzer acquires the following appearance:

$$\begin{aligned}&\mathscr{F}(\varphi_0),\ \mathbf{F}(\varphi_0/\varphi)=\\&=\arccos\left\{\frac{\sqrt{2}}{2}\,\frac{2-\gamma(t)\left(|\cos\varphi|+|\sin\varphi|\right)}{\left[(1-\gamma(t)|\cos\varphi|)^2+(1-\gamma(t)|\sin\varphi|)^2\right]^{1/2}}\right\}\end{aligned} \tag{5.8}$$

where $\gamma(t)$ are previously defined functions. The function of simultaneous contrast can be calculated using the formula:

$$\Delta\psi=\frac{1}{2}\left\{\arccos\frac{(1+\alpha^2)\cos\Delta\varphi-2\alpha}{1+\alpha^2-2\alpha\cos\Delta\varphi}-\Delta\varphi\right\}, \tag{5.9}$$

where $\Delta\phi$ is the difference in direction of motion of two point stimuli moving simultaneously and α is the coefficient of lateral inhibition between homonymous primary detectors of different local analyzers.

APPENDIX 6. STEREO ANALYZER

Primary detectors of stereo analyzer. The model of a stereo analyzer in question has the following structure. It consists of four independent monocular primary detectors of direction toward object with responses of the following type:

$$f_1(\alpha)=\sin\lambda_1\alpha,\quad f_2(\alpha)=\cos\lambda_1\alpha,\quad f_3(\gamma)=\sin\lambda_2\gamma,\quad f_4(\gamma)=\cos\lambda_2\gamma \tag{6.1}$$

and

$$f_5(\beta)=\sin\lambda_3\beta,\quad f_6(\beta)=\cos\lambda_3\beta,\quad f_7(\delta)=\sin\lambda_4\delta,\quad f_8(\delta)=\cos\lambda_4\delta, \tag{6.2}$$

where λ_1, λ_2, λ_3 and λ_4 are constants. Hereafter, it is assumed that $\lambda_1 = \lambda_2 = \lambda_3 = \lambda_4 = \lambda = \text{const}$, (α, γ) is a pair of horizontal and vertical angles that determine the "direction toward object" for the left eye. These angles are determined in relation to a certain fixed point Φ. The analogous angles for the right eye are (β, δ).

Primary depth detectors are formed from primary monocular detectors of direction of different eyes. The depth analyzers consist of primary depth detectors and a set of secondary detectors. The input signal for primary depth detectors is the difference between signals:

$$\Delta = \sin\lambda\alpha - \sin\lambda\beta \tag{6.3}$$

When angles α and β are rather small:

$$\Delta \approx \lambda(\alpha - \beta) \tag{6.4}$$

i.c., Δ is a horizontal disparity.

The primary detectors of the depth analyzer have the following characteristics:

$$\Delta f_1 = \sin\lambda_h\Delta u \qquad f_2 = \cos\lambda_h\Delta \tag{6.4a}$$

where λ_h are constants. Functions (6.4a) are components of the disparity vector

$$D = \{\Delta f_1, \Delta f_2\} \tag{6.5}$$

The distance of point A (4) in relation to fixation point Φ is coded in the local depth analyzer by the direction of vector D. This analyzer "services" a small sector of visual space. Other parts of this space are examined by other local depth analyzers. There can be significant overlapping of sectors of visual space of different local analyzers. Thus, the same point A can be seen simultaneously by several depth analyzers (Figures 68, 69). The question arises: In what cases does the "depth" of point A perceived by different local analyzers have the same value? Let point Φ_i (2) ($i = 0, 1, \ldots, m$) serve as the reference point for the ith local analyzer. Further, let the following angles be defined for this analyzer:

$$(\alpha_i, \beta_i) \text{ and } (\theta_i, \eta_i), \quad (i = 0, 1, \ldots, m) \tag{6.6}$$

where α_i and β_i are horizontal angles at which point A is seen with the left and right eye, respectively; η_i and θ_i are angles at which the zero depth analyzer sees reference point $\Phi_i(1)$. If the difference $\theta_i - \eta_i = \text{const}$, the disparity Δ_i of point A for all local depth analyzers has a constant value $\Delta = \sigma_i - \beta_i = \text{const}$ ($i = 0, 1, \ldots, m$).

Indeed, angles α_i and β_i can be expressed in the following manner (Figure 69):

$$\alpha_i = \alpha_0 - \theta_i \quad \text{and} \quad \beta_i = \beta_0 - \eta_i \tag{6.7}$$

Then $\Delta = \alpha_i - \beta_i = \alpha_0 - \beta_0 + \eta_i - \psi_i$. If

$$\eta_i - \theta_i = \text{const} = c \tag{6.8}$$

$$\Delta \simeq \alpha_0 - \beta_0 + c = \text{const} \tag{6.9}$$

In the special case, if $c = 0$, i.e., $\eta_i = \theta_i$, the reference points Φ_i are on the Fit-Muller circle.

Thus, if $\theta_i - \eta_i = \text{const}$, point A is perceived in all local depth analyzers as being at the same distance from line $\theta_i - \eta_i = \text{const}$.

When angles α and β are rather large, disparity Δ should be determined from expression (6.3). In this case, point A is perceived by all local analyzers as being at the same depth if all reference points are on a line along which the following condition is satisfied:

$$\Delta_i = \sin \lambda\alpha_i - \sin \lambda\beta_i = \sin \lambda(\alpha_0 - \theta_i) - \sin \lambda(\beta_0 - \eta_i) = \text{const} \tag{6.10}$$

If reference points Φ_i of local depth analyzers are situated along curve (6.10), the disparity of arbitrary point A seen simultaneously by several analyzers is a constant. To avoid discrepancy in depth analyzer readings in measuring the distance of point A, the eyes must be so oriented as to have all reference points corresponding to the centers of receptive fields situated on the horopter (6.10).

Properties of stereo analyzer model. The horopter as the geometric site of points having the same direction for the right and left eye separately: It is assumed that the monocular direction of the object is given by two independent vectors with components (6.1) and (6.2). The direction of the object is the same for the left and right eye separately if the corresponding excitation vectors are collinear to one another and the corresponding components of these vectors equal one another. If we consider that, in the horizontal plane, the difference between vertical angles of vision of the object with the left and right eye is insignificant, the equality of monocular directions of the object is determined by the condition:

$$\sin\lambda\beta = \sin\lambda\alpha \quad \text{and} \quad \cos\lambda\alpha = \cos\lambda\beta$$

Then

$$\alpha = \beta \tag{6.11}$$

Condition (6.11) is satisfied for all points on the circle traced through the fixation point and optical centers of both eyes (Fit-Muller circle).

The horopter as the geometric site of equidistant points in depth, and as the fixation point: Let us consider first the cases when the term "equidistant in depth" means that the object has zero depth in relation to the fixation point and disparity of the object equals zero. Vertical disparity in the horizontal plane is small, and it has no appreciable influence:

$$\Delta = \sin\lambda\alpha - \sin\lambda\beta = 0 \tag{6.12}$$

Then $\alpha = \beta$, which corresponds to a horopter in the form of a Fit-Muller circle.

In the case where the term, "equidistant in depth" means that point A is just as far in depth as fixation point Φ in relation to a certain reference point B, which is chosen on the cyclopian axis, we should alter somewhat condition (6.12). Let disparity of fixation point Φ in relation to reference point B be:

$$\Delta(\Phi/B) = \sin\lambda\alpha - \sin\lambda\beta = c \tag{6.13}$$

i.e., disparity vector $\mathcal{D}(\Phi/B)$ has components of the following appearance:

$$\sin\lambda_h\Delta(\Phi/B), \quad \cos\lambda_h\Delta(\Phi/B) \tag{6.14}$$

The points on the horizontal plane, for which disparity vector $\mathcal{D}(A/B)$ is collinear with vector $\mathcal{D}(\Phi/B)$, are just as far in depth from point B as the fixation point. These vectors are collinear if disparity (6.10) is constant for all of the indicated points, i.e.,

$$\sin\lambda\alpha - \sin\lambda\beta = c = \text{const} \tag{6.15}$$

Thus, the horopter as the geometric site of points that are at a constant depth away from point B in the horizontal plane is described by curve (6.15). Figure 70 illustrates horopters for different values of constants c (6.15) and with different positions of reference point B on the cyclopian axis.

Mixture effects in the depth analyzer: Let there be a given fixation point Φ and two points A and B on the cyclopian axis. The angle of vision of these points A and B in relation to fixation point Φ is the same for both eyes. The monocular vectors determining the direction of points A and B have the following appearance:*

$$\mathcal{F}_{\text{л}}(A) = (\sin\lambda\alpha,\ \cos\lambda\alpha,\ \sin\lambda\gamma,\ \cos\lambda\gamma), \tag{6.16}$$
$$\mathcal{F}_{\text{п}}(A) = (\sin\alpha_1\lambda,\ \cos\lambda\alpha_1,\ \sin\lambda\delta,\ \cos\lambda\delta), \tag{6.17}$$
$$\mathcal{F}_{\text{л}}(B) = (\sin\lambda\beta,\ \cos\lambda\beta,\ \sin\lambda\gamma,\ \cos\lambda\gamma), \tag{6.18}$$
$$\mathcal{F}_{\text{п}}(B) = (\sin\lambda\beta_1,\ \cos\lambda\beta_1,\ \sin\lambda\delta,\ \cos\lambda\delta). \tag{6.19}$$

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*Translator's note: In following equations subscripts п and л refer to right and left, respectively.

Further, let both points A and B be situated in the same receptive field and together excite the primary detectors. As a result, instead of vectors (6.16)-(6.19) we have vectors

$$\begin{aligned}\overline{\mathcal{F}_{\text{Л}\Sigma}} &= \overline{\mathcal{F}_{\text{Л}}(A)} + a\overline{\mathcal{F}_{\text{Л}}(B)} = \\ &= \{\sin\lambda\alpha + a\sin\lambda\beta,\ \cos\lambda\alpha + a\cos\lambda\beta,\ 2f_3,\ 2f_4\},\end{aligned} \tag{6.20}$$

where $0 \leqslant a \leqslant 1$ is the coefficient which takes into consideration the intensity of points A and B. If $a = 1$, the intensity of both points is the same, but if $a = 0$, the intensity of point B equals zero.

Analogously, for the right eye, the overall excitation vector is

$$\begin{aligned}\mathcal{F}_{\text{П}\Sigma} &= \mathcal{F}_{\text{П}}(A) + a\mathcal{F}(B) = \\ &= \{\sin\lambda\alpha_1 + a\sin\lambda\beta_1,\ \cos\lambda\alpha_1 + a\cos\lambda\beta_1,\ 2f_7,\ 2f_8\}.\end{aligned} \tag{6.21}$$

In view of the fact that, according to condition $\alpha = -\alpha_1$, $\beta = -\beta_1$ and $\beta = -\alpha$, instead of vectors (6.20) and (6.21), we get

$$\overline{\mathcal{F}_{\text{Л}\Sigma}} = \{\overline{(a-1)\sin\lambda\beta,\ (1+a)\cos\lambda\beta}\}$$

and

$$\mathcal{F}_{\text{П}\Sigma} = \{(1-a)\sin\lambda\beta,\ (1+a)\cos\lambda\beta\}. \tag{6.22}$$

Further, we calculate disparity of the resultant stimulus on the basis of vectors (6.21):

$$\Delta_\Sigma = 2(a - 1)\ \sin\lambda\beta \tag{6.23}$$

As a result, the disparity vector has the following appearance

$$D_\Sigma = \{\sin\Delta_\Sigma,\ \cos\Delta_\Sigma\} \tag{6.24}$$

Let now $a = 1$, i.e., the intensity of both stimuli is the same. Then, vector $D_\Sigma = (0, 1)$ is collinear with $D(\Phi) = \{0, 1\}$. In other words, the resultant stimulus is perceived at the same depth as the fixation point. Since disparity of the resultant stimulus equals zero, there will be fusion of both points. Ultimately, the model perceives the two points A and B at the same depth as the fixation point. With decrease in a the depth of the resultant stimulus changes: the resultant stimulus draws closer in depth to the brighter point, and with $a = 0$ the depth of the remaining point coincides with the depth of the overall stimulus. When there is significant change in brightness of one of the stimuli, the disparity of the overall effect increases to the extent of development of diplopia, when there is double perception of the image when the intensity of one of the points is low enough.

Analogous effects were described by Foley [16] in experiments on humans.

Anomalies of depth perception: The input signal for primary detectors of the depth analyzer is:

$$\Delta = \sin\lambda\alpha - \sin\lambda\beta \tag{6.25}$$

which may be either negative or positive, depending on the position of point A in relation to fixation point Φ.

In view of the fact that transmission of positive and negative signals over the same channel is impossible in biological systems, there must be separate channels for complete fulfillment of function (6.25): one to transmit a positive signal and the other to transmit a negative one. More precisely, we must have two separate primary detectors of disparity, which fulfill together the same function sin Δ. One of the primary detectors is excited only if $\Delta>0$, whereas the other is excited if $\Delta<0$, i.e.,

$$\Delta f_{11}=\begin{cases}\sin\lambda_{\hbar}\Delta, & \text{if } \Delta>0,\\ 0, & \text{if } \Delta\leqslant 0;\end{cases}\qquad \Delta f_{12}=\begin{cases}0, & \text{if } \Delta>0,\\ \sin\lambda_{\hbar}\Delta, & \text{if } \Delta\leqslant 0.\end{cases}\qquad (6.26)$$

$\Delta>0$ if $\sin\lambda_{\hbar}\alpha>\sin\lambda_{\hbar}\beta$ or $\alpha>\beta$. Analogously, $\Delta<0$ if $\alpha<\beta$. In other words, a detector with a response of the Δf_{11} type is excited only if the angle of vision of the object with the left eye is larger than the angle of vision of the object by the right eye. For this primary detector, the left eye has an excitatory effect and the right, an inhibitory effect. By analogy, detector Δf_{12} (6.26) is excited by the right and inhibited by the left eye.

If, however, one of the detectors, Δf_{11} or Δf_{12}, is lacking, the system will be incapable of perceiving the depth of stimuli that have either positive or negative disparity. In the model, this means that it will be incapable of estimating the depth of stimuli that are either farther away than the fixation point or stimuli that are closer than the fixation point.

The secondary depth detectors have selective responses that are similar to the stereo detectors of the vertebrate visual cortex.

APPENDIX 7. POLARIZED LIGHT ANALYZER

It is assumed that there are three primary detectors at the input of the polarized light analyzer, two of which are sensitivity to inclination of the plane of light polarization, while the third detector does not have selectivity for polarized light. According to Bernard and Wehner, in the inset retina there are direct receptors which have selectivity to the inclination of polarized light plane by virtue of their internal structure. The responses of such receptors have the following appearance:

$$r_1(\varphi)=[1+A\cos 2(\varphi-\varphi_1)] \tag{7.1}$$

and

$$r_2(\varphi)=[1+A\cos 2(\varphi-\varphi_2)], \tag{7.2}$$

where A is a constant that depends on degree (depth) of polarization; ϕ is the angle between the polarization plane and horizontal plane; ϕ_1 and ϕ_2 are the values of angle ϕ that maximize the response of the first or second receptor, respectively. According to Wehner:

$$|\phi_1 - \phi_2| \cong 45°$$

One can obtain primary detectors of the polarized light analyzer by subtracting from $r_1(\phi)$ or $r_2(\phi)$ a constant, $a = 1$. As a result, the responses of primary detectors have the following appearance:

$$f_1(\varphi)=A\cos 2(\varphi-\varphi_1), \qquad f_2(\varphi)=A\cos 2(\varphi-\varphi_2). \tag{7.3}$$

$$f_3(\varphi)=A.$$

If we consider that a detector cannot transmit a negative quantity, the number of selective detectors will double. Their characteristics can be realized as follows:

$$f_{10}=\begin{cases} r_1(\varphi)-1=\cos 2(\varphi-\varphi_1), & \text{if } -\pi/2\leqslant 2(\varphi-\varphi_1)\leqslant \pi/2; \\ 0\text{— otherwise;} \end{cases}$$

$$f_{11}=\begin{cases} 0, & \text{if } -\frac{\pi}{2}\leqslant 2(\varphi-\varphi_1)\leqslant \frac{\pi}{2}; \\ -r_1(\varphi)+1=-\cos 2(\varphi-\varphi_1)\text{—otherwise;} \end{cases}$$

$$f_{20}=\begin{cases} r_2(\varphi)-1=\cos 2(\varphi-\varphi_2), & \text{if } -\frac{\pi}{2}\leqslant 2(\varphi-\varphi_2)\leqslant \frac{\pi}{2}; \\ 0\text{— otherwise;} \end{cases}$$

$$f_{21}=\begin{cases} r_2(\varphi)-1=\cos 2(\varphi-\varphi_2), & \text{if } -\frac{\pi}{2}\leqslant 2(\varphi-\varphi_2)\leqslant 3\frac{\pi}{2}; \\ 0\text{—otherwise.} \end{cases}$$

Thus, polarized light is characterized by the direction of the excitation vector:

$$\mathcal{F}(\varphi)=(f_1(\varphi),\ f_2(\varphi),\ f_3(\varphi)),\ \text{where}$$

$$f_1(\varphi)=\begin{cases} f_{10}, & \text{if } -\frac{\pi}{2}\leqslant 2(\varphi-\varphi_1)\leqslant\frac{\pi}{2}; \\ f_{11}, & \text{— otherwise;} \end{cases}$$

$$f_2(\varphi)=\begin{cases} f_{20}, & \text{if } -\frac{\pi}{2}\leqslant 2(\varphi-\varphi_2)\leqslant\frac{\pi}{2}; \\ f_{21} & \text{— in other cases.} \end{cases}$$

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