

A REVIEW OF THEORY IN PHYSIOLOGICAL PSYCHOLOGY¹

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INTRODUCTION

The impact of recent technical advances on the subject matter of neurophysiology and neuropsychology is not limited to the accumulation of data. Ways of looking at the functions of the central nervous system in behavior keep pace with the detail of facts. Neuropsychological data were extensively reviewed in these volumes only last year (130); data from the adjacent fields of sensory psychology (61, 68, 127), psychochemistry, and psychopharmacology (98, 124, 154) are covered in several sources. But no recent review of "theory" in physiological psychology is readily available. Thus, this fascinating, though difficult, topic is chosen for discussion. In keeping with the policy of the *Annual Review of Psychology*, a considerable degree of selectivity in acceptance and rejection of material for review has been exercised; and several outright speculations that reveal the author's biases are included.

BASIC FUNCTIONS OF CENTRAL NEURONAL AGGREGATES

During the first half of this century the predominant view of neuronal aggregates, or "brains," has been that they constitute essentially passive, inert masses of specialized tissue sensitive to excitations propagated to and from them by nerve trunks. Alterations in patterns of excitation between input and output were conceived to be the result of stable and specific geometrical configurations of connections established, for the most part, as a result of experience. This view was developed into what has become neuron and reflex-arc theory as expressed, for instance, in Sherrington's lectures published under the title, *The Integrative Action of the Nervous System* (136). However, the spatial, geometrical pattern of connections was never conceived as the only explanatory principle in reflex-arc theory; even at the relatively simple level of complexity of the interaction of spinal reflexes Sherrington invoked the concepts of central excitatory and inhibitory states and of simultaneous and successive spinal induction. These properties of the reflex arc were attributed to presumed discontinuities between neural elements—the synapses. Studies of synaptic processes proceeded, but, in their effect on behavior theory, they were overshadowed by the less elusive all-or-none properties of neural tissue—those involved in impulse transmission. Gradually, however, synaptic processes and their counterparts in axons

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(electrotonic phenomena) and dendrites (dendritic potentials) have pre-empted attention; today any realistic view of the functions of central neuronal aggregates must take these data into account. In addition, a considerable amount has been learned about the background of the neural activities into which any environmental stimulus must intrude in order to be effective.

INTRINSIC RHYTHMS

A series of carefully controlled studies from the Burns laboratory (23) has contributed some definitive answers to an age-old question: What happens when brain tissue is completely isolated neurally from other nervous tissue? The answers are, as they so often are, neither completely supportive of the notion that central activity is basically "spontaneous" nor entirely supportive of the axiom of a *tabula rasa*. Burns found that, even in the unanesthetized animal, the isolated cortical slab remains quiescent unless stimulated, although there are some other reports (39, 48, 65, 69, 88) that indicate that spontaneous activity may be present occasionally and temporarily. In any case, a few strong electrical stimuli applied to the cortical surface will produce a series of bursts of neural activity which usually continue for many minutes after stimulation has stopped. If a series of 10 such stimuli are given at intervals of three seconds each, neurons continue to discharge throughout the slab for as long as an hour.

The periodic waves of excitation that follow a few infrequent stimuli given to the unanesthetized cerebral cortex are also found to occur whenever diffusely organized nervous tissue is stimulated. Long-lasting effects have been observed after brief stimulation in the intact sea anemone—effects lasting many hours (11). Recently the luminescence response of sea pansies (a colorful soft coral) has been described as follows. After a series of stimulations, these colonies begin to luminesce spontaneously instead of doing so only in response to stimulation (22). To explain this behavior, a slow change of state in the neural tissue (a form of memory process?) must be invoked. These changes of state are accessible to environmental influence and are, of course, influenced by the previous activity of the organism, but they have intrinsic properties and their own time course of activity that determine recurrence apart from the environment of the moment.

In short, neuronal aggregates of the type found in the cerebral cortex are quiescent in the absence of continuous input. However, these aggregates are easily aroused to prolonged activity. Hence, at "rest," they may be conceived to be just below the excitatory level for continuous self-excitation. In the intact mammal, a mechanism exists to insure excitation beyond such a resting level. This mechanism is the spontaneous discharge of receptors.

Granit (55) has detailed how, gradually, "the idea of spontaneous activity as an integral part of the performance of sensory instruments has grown upon us." He traces the history of the subject from the early observations of Adrian & Zotterman (4) and of Adrian & Matthews (2, 3) on muscle and on optic nerve preparations to his own extensive experimental analyses. In addition, he cites evidence to support the suggestion that this "spontaneous activity of sense organs makes them one of the brain's most important 'ener-

gizers' " or activators. Granit posits that the nonmodality-specific reticular systems of the neuraxis, which receive branches from various sensory afferents in their passage upward, are the locus of the activating mechanism.

THE FEEDBACK UNIT—AN ALTERNATIVE TO THE S-R REFLEX ARC

The description of the dependencies between central neuronal aggregates and receptor activities is incomplete, however, if the relation is considered only as strictly one-way traffic. Livingston (91) and Granit (55) have thoroughly reviewed the large body of evidence that receptor activities are under efferent control from the central nervous system. With respect to muscle spindles, one-third of the efferents in the ventral spinal root serve this function (84, 85). In the optic and otic systems (45, 54), experiment has shown that the afferent activity originating in the receptors can be directly modified by central nervous system excitation. These facts make it difficult to maintain any longer the uncomplicated view of the functions of the central nervous system in behavior that are based on the simple S-R reflex arc. Bruner (21) has suggested some of the ways that psychology could be enriched by taking into account these new data. It is worthwhile, therefore, to re-examine for a moment the concept of the reflex arc and to see whether a useful alternative to this war horse can be found.

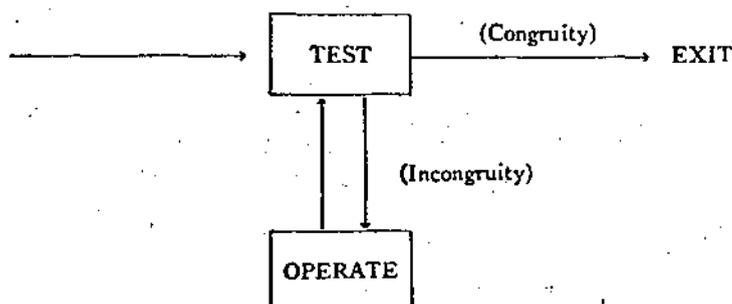
Sherrington, more than anyone else, is responsible for the popular conception of the reflex arc. Yet Sherrington (136), more than any one else, cautions again and again against oversimplification: "The simple reflex arc is a useful fiction"—used by Sherrington to explain the behavior of the spinal preparation. The most quoted example of the "simple" reflex is, of course, the stretch reflex, e.g., the knee jerk. Sherrington expressly states that he does not conceive this reflex to be an example of his "simple" reflex. Indeed he questions whether the stretch mechanism is a reflex at all. The reflex arc was invented by him to explain the difference between the observed properties of nerve trunks and the properties that had to be inferred to describe the neural tissue that intervenes between receptor stimulation and effector response. Nerve trunks transmit in either direction; characteristically, signals are of the all-or-none type. Reflex action, on the other hand, is unidirectional and is characterized by graded response. Sherrington explained the differences by espousing the neurone doctrine. This doctrine proposes that the nervous system is made up of discrete neural units (cells) which have the properties of nerve trunks; intercalated between these units are discontinuities which he christened synapses, and these have the properties unique to reflexes. In Sherrington's discussion of the interaction of reflexes, these synaptic properties become complicated indeed. Central excitatory and inhibitory states, simultaneous and successive spinal induction, and convergence and divergence of pathways are only a few of the most important intervening variables he postulated to explain reflex action of the spinal preparation. These properties are a far cry from the ubiquitous S-R reflex-arc diagrams that grace (more appropriately, one wants to say "disgrace") today's texts.

The evidence that receptors are under efferent control from the central nervous system makes possible a revision of the reflex-arc concept that is at

the same time more in keeping with the data and is definitely in keeping with the richly flexible nervous system that the psychologist needs if he is to have any useful conception of what goes on in the central nervous system during behavior. Since World War II, communications and control engineers have publicized the utility of a device that "feeds back" to a sensing mechanism the results of the actions of the machine of which the sensing mechanism is a part. This device is called the simple servomechanism, and neurophysiologists were quick to see that many of the processes that they had been studying in the central nervous system have the properties of simple servos (33). In fact, the central regulation of receptor activities makes it necessary to conceive of even the simplest reflex mechanisms in these terms.

What are the essential differences for psychology between the S-R reflex-arc concept and the simple servomechanism concept? Most important is a shift in emphasis. The shift is from the notion that an organism is a relatively passive protoplasmic mass whose responses are controlled by the arrangement of environmental stimuli to a conception of an organism that has considerable control over what will constitute stimulation. This control is exercised both through regulation by central processes and through a double feedback to receptors from response through environment and through the nervous system. Anyone who has spent any effort on the intricacies of "shaping" an animal or human preparatory to an operant conditioning experiment should sympathize with the validity of this shift in emphasis.

In detail, then, the alternative to the simple S-R notion of the reflex arc is a double mechanism that is constituted of one neuronal aggregate that is sensitive to a variety of inputs and another aggregate that is reciprocally connected to the first and effects the changes initiated by the first. Peripherally, the sensing mechanism includes the receptor; the effecting mechanism, the muscles and the glands. Miller, Galanter & Pribram (101), among others, have developed in detail the idea that the essential characteristic of the sensing mechanism is to test for incongruities and that the essential characteristic of the effecting mechanism is to operate on other units (that may include the environment) so as to decrease incongruity in the sensing mechanism. They speak of this sequence as Test-Operate-Test-Exit (TOTE) and suggest that this, rather than the S-R reflex arc, is the basic unit that controls action. A diagram of the simple feedback unit looks like this:



GRADED-RESPONSE MECHANISMS

In the S-R reflex-arc conception of the control of action, the importance for psychology of graded response mechanisms was confined pretty largely to the synapse. How are graded responses treated today? Bishop (15), in a definitive review that discusses the "natural history of the nerve impulse," states that "the chief and most characteristic functions of neurons and other excitable tissues are performed by means of graded responses." He suggests that graded responses are "more general as well as more primitive than the all-or-none response and that the latter probably developed when an early metazoan became too large. . . ." The author reviews the evidence supporting the contention that the cerebral cortex "still operates largely by means of connections characteristic of primitive neuropil, the most appropriate mechanism for the maintenance of a continuous or steady state, as contrasted to the transmission of information about such states." The dendrites, rather than the "impulsive axon," are probably the essential elements of graded response tissue. Axonic transmission of nerve impulses is conceived to transmit information about the continuous, steady state of excitability maintained by graded response tissue.

Upon what evidence do these heretical views rest? Should the "all-or-none" law be modified in favor of an "all-or-something" law? That graded response mechanisms exist in neural tissue is not news, of course. Electrotonic potentials and synaptic potentials have been studied for some time. The importance of graded dendritic potentials is news, however. The discovery came about in the following way. Li, Cullen & Jasper (87) and Bishop & Clare (16) were making use of the newly discovered microelectrode technique to investigate an important problem: How are the potential changes observed by means of the electroencephalogram generated? The common notion was that the recorded changes reflected some envelope of the impulsive activity of neural elements. The results of the studies indicated that such was not the case: the changes recorded by the electroencephalogram or electrocorticogram show a variation which is relatively independent of the number of impulses generated by the neurons sampled at the site of recording. And when recordings are made from the separate layers of the cortex, the potential changes that correlate with the electroencephalogram are those that are obtained from layers rich in dendrites. Investigations in this area are so recent (146) that very little is yet definitely known of the functional significance for behavior of these graded response mechanisms of neural tissue. Nor are the impulsive aspects of neuronal activity to be ignored—but theories about these will be dealt with in the last section of the review. In this context, one cannot but call to mind the pioneer work of Barron & Matthews (10), of Gerard & Libet (47), and of Skoglund (139), who showed that neuronal aggregates are sensitive to graded (direct current) electrical stimulation and that this sensitivity is differential with respect to polarity and the like. Köhler (83) has recently reviewed these experiments and those performed under his direction, and has used these data to develop his field notions of

neural action in perception. Could it be that the sensitivities to graded stimulation and the graded response mechanisms are the characteristics essential to the test phase that goes on within the neuronal aggregates that serve as the simpler TOTE units?

In summary, then, some very old questions have received limited but definitive answers. The brain, though in some ideally abstract way quiescent unless stimulated, becomes intrinsically active for prolonged periods after even momentary excitation. That this excitation is provided by the afferent connections from receptors is not surprising; what is new is the finding that receptors are spontaneously active even in the absence of stimulation from the environment. Furthermore, the spontaneous receptor activity is not only influenced by environmental events but is also under centrifugal control from the central nervous system. These facts make it necessary to replace the simple S-R reflex-arc concept. The notion of the simple servomechanisms, borrowed from communications and control engineering, is the most logical and useful replacement. The servo is conceived to act as a Test-Operate-Test-Exit (TOTE) sequence accomplished by two reciprocally connected neuronal aggregates. One of the aggregates performs the test functions; when incongruities of inputs occur in the test, control is shifted to another neuronal aggregate that operates on other neural mechanisms or on the environment, or on both, until the incongruities of the test are resolved. Graded response mechanisms, originally attributed primarily to synapses, have been found to be an important characteristic of all central neural tissue. These graded response mechanisms may play an essential role in the test phase of the simpler TOTE sequences.

FUNCTIONAL LOCALIZATION IN THE CENTRAL NERVOUS SYSTEM

THE CONCENTRIC NERVOUS SYSTEM

During the past decade there has been an important change in the way in which experimentalists have approached the analysis of the central nervous system. Earlier studies had, for the most part, supplied horizontal divisions: the spinal animal, the *encephale isolé*, the decerebrate and decorticate preparations. Such laws as "progressive encephalization" of functions during phylogenesis and the "control of lower neural levels by higher ones" resulted from these studies.

More recently, analysis has become vertical. At the mesencephalic level, the Magoun group (97) has focused on the differences in organization and function of the reticular core, on the one hand, and the classical relay mechanisms of the more external portions, on the other. At the diencephalic level, Jasper (73) and his group have concentrated on clarifying the functions of the midline and intralaminar systems of the thalamus, functions that were initially described by Dempsey, Morison & Morison (34) and others. Several groups of investigators converged on the hypothalamus, another midline

diencephalic group of structures, to demonstrate some similarity of function between it and the mesencephalic and dorsal thalamic mechanisms. Finally, a group of investigators, sparked by Fulton (44), followed up the findings of Klüver & Bucy (82) and of Bard & Mountcastle (9) to differentiate the functions of the medial and basal "limbic" formations of the forebrain from those of the more laterally located portions of the cerebral mantle. These analyses have provided a conception of a nervous system built "from the inside out"—and some new laws can be stated that describe the properties of this concentric nervous system.

The internal core of the brain stem: biased homeostats and theories of drive.—Over a century ago, Bernard (13) initiated a branch of neurophysiology that is concerned with the regulation of the organism's metabolism and endocrine functions by the central nervous system. These now famous "picure" experiments, in which diabetes was produced by making small stab wounds in the brain stem, led Bernard to the conception of a *milieu intérieur* that is still central in the thinking of modern neurophysiologists [e.g., the reviews by Colle, Gasteaut & Dell (32)]. Somewhat less well known are the extensive series of experiments by Karplus (76) and Karplus & Kreidl (77, 78, 79) performed at the beginning of the century. These experiments thoroughly explored the relations between diencephalic centers and the regulation of visceral activities. More recently, this branch of neurophysiology has been advanced by Cannon's (25) formulation of the concept of homeostasis and by the laboratory analyses that occupied him and his collaborators. Another group of experimentalists, directed by Ranson (125), explored the relations between hypothalamic mechanisms and the maintenance of body temperature and food intake and activity. Contemporary investigations of the thirst mechanisms (60), of endocrine control (60, 66), and of respiratory regulation by the partial pressure of CO_2 in the brain-stem respiratory center (100) are only some of the highlights in this area of investigation.

In spite of the variety of arguments against the notion, these experimental results have tended to confirm the idea that specific centers exist in the central nervous system to control one or another of the metabolic and endocrine activities of the organism. Most of the evidence against centers has come from studies that deal with parts of the central nervous system other than these centrally located regions in the brain stem and with behavior other than that involved in the regulation of the organism's metabolism. What, then, characterizes these structures; what makes them different from other central neuronal aggregates? The most useful way to look at this difference seems to revolve around the specific sensitivities of these centers to one or another physicochemical substance. And this is exactly how receptors are defined in the peripheral nervous system.

The conception that receptor mechanisms may be located around the midline ventricles of the brain stem derives support from two sources. The experiments already alluded to have produced data that are consistent with the concept of homeostasis. Any homeostat must include an element that is

especially sensitive to the range of physical (or chemical) events that the homeostat attempts to regulate. In the case of the brain-stem homeostats, this sensitive element could be entirely located in the peripheral mechanism that is afferently connected with the central nervous system, but experiment has demonstrated that at least some of the sensitivity is located centrally, e.g., hypertonic saline injected into the third ventricle immediately causes goats to drink voluminously (6); heat applied to the base of the anterior extremity of the third ventricle immediately causes changes in the heat regulating mechanisms all over the body (125); very local changes in the partial pressure of CO_2 in the posterior brain stem dramatically alter the rate and depth of respiration (100). All of these sensitivities are specific and restricted to very small regions, and all are localized to structures fairly near the third and fourth ventricles of the brain stem.

The second source of support for the conception that receptor mechanisms might be located near the midline ventricular system is less direct. Ontogenetically, this median part of the central nervous system is derived from the most dorsal part of the neural crest: invagination to form the neural tube makes the periventricular components those most akin in origin to the epidermal portions of the ectodermal formations. And it is these portions of the ectoderm that induce some of the more specialized of the receptors, such as the retina. Furthermore, the sensitivities of the periventricular mechanisms are very similar to those of the skin. Temperature change, deformation, and changes in hydration are some of the major categories of stimuli to which both are sensitive.

In summary, then, the work of a century of neurophysiological experiment seems to be leading to the conception that a series of specialized receptors are located near the midline ventricular systems of the brain stem. These specialized receptors are the classical centers for the control of respiration, food intake, etc., that have interested physiologists and biochemists concerned with the neural regulation of the organism's metabolism and endocrine functions. These receptors are conceived to function as sensitive elements of a variety of homeostats concerned with the regulation of appetitive-consummatory processes.

Immediately beyond the limits of the periventricular receptor centers lies a matrix of neural reticulum spotted here and there with neuronal aggregates and coursed only occasionally by long nerve fibers. The anatomy of the brain stem reticular formation has been detailed by Brodal (20), and by the Scheibels (132); its physiology is well documented in a recent symposium (126) and by Magoun (97) in his Salmon lecture. Characteristically, the reticular systems are composed of fairly short, fine-fibered neurons with vast dendritic networks. Inputs converge on each nerve cell from many branches of the long classical projection tracts that originate in the various receptor fields of the organism. Each neural element in the system is influenced by a variety of sensory modes indicated by changes in the electrical activity as recorded with microelectrodes. In addition, a reciprocal relation with the

rest of the neuraxis exists, e.g., the cerebral cortex is activated when the brain-stem reticular formation is electrically excited and, conversely, cortical stimulation affects the activity of the reticular systems. This convergence of input and diffuseness of interrelations suggests that the most likely action of these systems is to influence the general state of excitability of the nervous system. This suggestion is supported by the finding that cortical rhythms are activated and deactivated by electrical stimulation of the reticular formation and by the fact that lesions and stimulations of these systems have been shown to be related to such behavioral processes as the sleep-wakefulness cycle, alertness, and attention. Furthermore, the anatomical structure of these systems is of a kind that suggests graded response mechanisms rather than signal transmission. Synapses and dendrites are abundant; fibers are, for the most part, short and fine so that the conduction velocity of an impulse is slow and its amplitude small. Such graded response mechanisms are especially sensitive to changes in their chemical environment; a great number of studies have related the action of neural transmitters and psychopharmacological agents to the functions of these systems (18, 40). Their proximity to the more specialized periventricular receptors is therefore significant to the problem of the "homeostatic" regulation of the organism's *milieu intérieur*, ordinarily referred to by psychologists as mechanisms of drive.

A considerable literature has developed recently with regard to the role of the reticular systems and their forebrain extensions in the regulation of drives. Lindsley (90) and Hebb (62), especially, have spelled out the details of "activation" theories based on neurophysiological evidence. Some constructive criticism of these views has come from investigators who have explored the internal core systems and their forebrain extensions. These investigators have been impressed with the selective action of various locations on specific drive mechanisms. The formulations of central excitatory mechanisms or central motive states as proposed by Beach (12) and by Morgan (111) lean in this direction. The studies of Teitelbaum (147) and of Stellar (144) on the hypothalamic control of feeding and the regulation of thirst and hunger by Miller (103) fall into this category. Most explicit in opposition to an activation theory, yet somewhat different from the selection notion, have been the statements of Olds (115), who has interpreted the data that have resulted from self-stimulation experiments to mean that a central hedonistic mechanism exists. Since animals will work to produce electrical excitation in parts of their brains and will work to stop such stimulation in other parts, a neural "pleasure system" and a neural "displeasure system" are postulated; the "pleasure system" is subdivided into portions that deal differently with sex and hunger. Furthermore, Olds has proposed that the pleasure system works as a positive feedback mechanism, so that an organism's pleasurable activity is stopped only when restraints external to the organism are imposed.

Each of these formulations is based on a particular set of data; each ignores, for the most part, the data upon which the alternate proposals are

based. All of these recent theories share a view that is essentially nonhomeostatic. Activation, selection, and hedonism all emphasize direction rather than equilibration. Attempts have been made to reconcile direction with equilibration. Miller's discussions of the cue properties and the drive properties (conceived in need-reduction terms) of stimuli are probably the best known of these attempts.

Taken together, the neurophysiological and behavioral evidence seems to add up to the view that both an equilibratory and a directional component characterize drives, and that selection, activation, and equilibration are all important. However, hedonism need not be invoked, nor need one consider the selective or cue properties of stimuli as the sole directional components of drive. A simpler view can be formulated. Consider the various elements that make up a homeostat. The sensitive element has already been mentioned, i.e., a homeostat must contain a receptor that is selectively sensitive to the physical or chemical process that is to be regulated. Such receptors exist in the central nervous system. A homeostat is essentially a feedback unit. As such, it must be so constituted that errors in adjustment are fed back to the sensitive element in time for this to signal the disparity to the operate mechanism. Ample neurophysiological and behavioral evidence exists that negative feedback mechanisms exist. After all, this is the evidence upon which the concept of homeostasis rests. But, in addition to these elements of the homeostat, there is another which has been largely ignored. Negative feedback mechanisms are usually equipped with a device by which their bias can be set, e.g., the thermostats in our homes can be set to one or another temperature. The activating mechanisms and electrical self-stimulation can be thought of as changing (by alterations in graded response mechanisms) the biases of the various homeostats with which they are anatomically juxtaposed. The laws that govern the changes in biases would be different from those that govern regulations once the biases have been set. For instance, small increments of change in bias are apt to be accommodated smoothly and are likely to be directional; more abrupt changes are apt to cause marked fluctuations until the regulatory mechanism can again re-establish equilibrium. No simple hedonistic rule can be applied, i.e., behavior is not always guided toward some pleasurable consequence. Selection of stimuli depends on the state of the receptor. Activation shifts biases. Equilibratory homeostasis in the classical sense (and thus need-reduction) is seen as only one phase, the equilibrational, of a rather more complex process. Basic to this process is the up-to-date neural homeostat constituted of a receptor, negative feedback, and bias. Thus the essential mechanism of drive is conceived to be a biased, i.e., a tuneable, homeostat.

The limbic endbrain: multilinked homeostats and dispositions.—Along the innermost edge of the cerebral hemispheres lies a series of structures which, though they differ considerably from each other, share the attribute that they are unlike the rest of the cerebral mantle. Broca gave a unitary name to this conglomerate core of the endbrain, a name which has become ac-

ceptable through usage—the limbic systems. The term is a good one since it does not impute function where function is not known (e.g., rhinencephalon is another name loosely applied to many of the same structures and has the disadvantage that these structures are only remotely related to the nose and to smell). Because of the anatomical diversity within the limbic systems, some anatomists have been loath to make the grouping in this particular way; because of similarities in function, physiologists have stretched the boundaries of the territory so that now one hears that parts of the core of the brain stem should be considered within the limbic systems. Actually, the problem of classification is not so terribly difficult. Within the endbrain, those formations that are usually called limbic can be distinguished on the basis of a precise histological criterion and the classification validated by a variety of equally precise indices (122). Similar classificatory procedures have not as yet been applied to the core structures of the brain stem, so at the moment there is bound to be some confusion. When this becomes sufficiently painful to the neuroanatomists, one of them will, no doubt, undertake the equally painful process of making order out of the present chaos.

What are the functions that have so excited neurophysiologists that they pursue them into the deepest recesses of the brain? The drive-regulating neural mechanisms found in the core of the brain stem have been one source of the challenge. Those which are related to the internal aspects of the end-brain have been more elusive, but equally fascinating. The trouble stems from the fact that a wide variety of seemingly unrelated effects on behavior results when any one of these structures within the limbic endbrain is electrically stimulated or surgically destroyed. Two different points of view have been adopted in the various attempts to categorize the observations: (a) The limbic systems are the substrata concerned with motivational and emotional behavior, motivation and emotion being conceived as primitive, instinctual, visceral reactions; (b) The limbic systems are primarily concerned with memory. Clinical and experimental observation can, of course, be advanced to support both of these interpretations. But these views cannot both be entirely correct since they refer to different sets of data and neither encompasses the data that the other seeks to cover. A review of some of the data will point up the limitations of the current formulations and prepare the ground for a more adequate explanation.

Neurobehavioral studies performed on animals have provided a major source of data. Ablation and stimulation of any of the various structures that make up the limbic systems interfere with a variety of behaviors. These data have been detailed in several recent publications. In order to remain uncommitted with respect to one or another theoretical position and yet have a pedagogically useful categorization, some neutral label that describes this behavioral complex of feeding, fleeing, fighting, and sex, might well be invented. Feeding includes such aspects as hoarding; sex includes mating and maternal manifestations. These data have been used to support the notion that the limbic systems serve motivation and emotion. But when this

notion is examined carefully, the support is seen to be spurious. If motivation and emotion are conceived to be viscerally determined reactions, the limbic systems ought to be primarily concerned with visceral regulation. Indeed, the limbic systems have been called the "visceral brain" (92, 94) in order to emphasize this relation. And special relations with the autonomic nervous system and the viscera do obtain. But these are not selective; other parts of the cerebral mantle (e.g., the motor cortex) also control autonomic and visceral activities and the control which the limbic systems exercise is certainly not limited to viscera or the autonomic nervous system.

An alternate hypothesis has therefore been proposed to account for data in terms of the emotion-motivation notion. This alternative has not always been clearly separated from the visceral hypothesis; often both are invoked (93), the one to account for some facts and the other to be used as soon as the first fails. This second hypothesis is that the limbic systems serve instinctual, innate patterns of behavior, phylogenetically and ontogenetically old (57). Support for this hypothesis comes from comparative neurology, since some of the structures included in the limbic systems are among the oldest to be found in the endbrain. But this hypothesis also fails to be supported upon close scrutiny. All of the structures in the limbic systems are not old: some are accretions as phylogenetically recent as to appear first in primates. And behavior such as fleeing, tested in a conditioned avoidance situation, is learned and highly specific to the situation. Abnormalities of sexual behavior produced by limbic system lesions in cats have been shown to depend not on hypersexuality per se but on the differences between normal and operated cats as to where, i.e., the territorial range, sexual behavior takes place. The experiential components that determine this sort of behavior are not to be ignored. Neither hypothesis is adequate; therefore, the limbic systems cannot be conceived as the neural substrata of motivation and emotion if these are thought of exclusively in terms of visceral-autonomic activities nor if they are felt to be old, primitive, innately determined processes (117). The search for an adequate explanation must continue.

The neurosurgical clinic has inadvertently produced another set of data that bear on this problem. By no stretch of imagination can these data fit simply the rubrics of motivation or emotion. Extensive resections of the medial structures of the temporal lobe of the brain of man, the amygdaloid and hippocampal formations of the limbic systems, result in a very peculiar and dramatic syndrome (104). Patients with such lesions are able to repeat correctly a series of digits that they have just heard for the first time. On this test of immediate memory they are practically as efficient as they were before the lesion was made. Moreover, their memory for events prior to their surgical operation is apparently normal. And they are capable of reacting emotionally in trying situations. But, if distracted, these patients are unable to carry out a sequence of actions, i.e., they are unable to recall what they are supposed to do. If there is an interruption of a test procedure, the patient will not only be unable to continue where he left off; he will, in fact, not even

recall that there was any task at all. If the examiner should be called from the room for a quarter of an hour, the patient will fail to recall that he had ever seen the physician before. This patient can be directed to a grocery store where he can purchase the items on a written list without having to refer to that list any oftener than would a person with an intact brain. But once he has completed the shopping, the patient does not recall what he is supposed to do next and he is completely incapable of finding his way home.

Memory is a complicated affair. Not only must the engram be recorded and stored, it must also be accessible when it is appropriate to the occasion. The syndrome shown by these patients can be summarized by the statement that the patients are unable to recall whatever is necessary to execute a sequence of actions. Given an external plan written out on a piece of paper, the patient can carry on quite well. Where in the memory process the difficulty lies can only be guessed at present; such guesses have been made (26).

On the surface the defect shown by these patients would seem to have little in common with the disturbances noted in the animal experiments. Perhaps a deeper analysis can show that some common elements between them exist. The element common to the activities of feeding, fleeing, fighting, and sex is that they are all comprised of sequences of acts (117). Their disturbance by limbic system lesions depends on the locus of the lesion. After amygdalotomy, the threshold for initiating the sequence is high and the behavior runs inappropriately long once it has been initiated (152). Feeding behavior may be difficult to initiate; once it has started it is difficult to stop. After median cortex lesions (cingulate), the maternal behavior of rats is peculiar (142). When a normal mother rat is faced with a situation in which her brood has been strewn around the cage, she will pick up one baby at a time and carry it to the nest, go back to pick up another and return it to the nest, and so forth, until all of the youngsters are safely back in the nest. The lesioned mother rat will pick up an infant, carry it to the nest only to remove it on subsequent trips. After half an hour of this the baby rats are still strewn all over the cage and, eventually, are left to die. What would happen if the mother rat could read, the babies were labelled, and the mother given a written list of directions to plan the retrieval of her brood?

The element common to both the patients with limbic system resections and the animals who show disturbances of the four activities mentioned above seems to be in the execution of certain sequences of actions. Deficiencies appear where the execution depends on some fairly complex plan that has to be carried inside the head. Thus, limbic system lesions can be thought to interfere with behavior because of some defect in the planning mechanism, and not because of disturbed emotion or motivation, nor primarily because of some global defect in memory. Limbic system function is thus conceived to be related primarily to the mechanism of the execution of complex sequences of action.

Analysis of the neural mechanism that underlies the execution of sequences of actions has just begun. Electrical changes have been recorded

from the amygdaloid complex of the limbic systems whenever the organism is exposed to a novel event or one that has meaning in terms of reward and punishment (26, 75). These electrical changes subside once the organism is familiar with the event unless the hippocampal formation of the limbic systems has been ablated, in which case electrical changes continue to occur when this or any other event takes place. The amygdaloid complex is necessary to the establishment of electrocortical conditioned responses. The suggestion has been made that the hippocampal formation inhibits (perhaps by way of the reticular core of the brain stem) the succession of unrelated inputs to the amygdala that might occur and so allows this structure to maintain the neural activity necessary to the conditioning process. In a conditioning or learning situation, electrical changes are recorded from the hippocampal formation during the initial trials; later, no such changes accompany successful action; they occur only when errors are made (1).

These characteristics of limbic system function will again be met later in this review in the discussion of simulated brains. Essentially, when a series of biased homeostats is interconnected, either randomly or hierarchically, and the interconnections have the property of feedback, an ultrastable system results. Such an ultrastable system returns to some predetermined state in the face of perturbations caused by inputs to the component biased homeostats, or by local changes that may result for one or another reason in any one of the components. The system is said to show a disposition to return to the state and to be especially sensitive to error, i.e., to changes in the bias of the components that tend to cause deviations of the system from that state. The interconnections of the limbic forebrain systems with each other and with the structures of the diencephalic and mesencephalic internal core anatomically fulfill the requirements for an ultrastable system. The large tracts that connect the amygdaloid complex and the hippocampal formation with the septal region and the anterior and posterior hypothalamus are well known. The tracts that connect the limbic areas with the mesencephalic reticular core have been emphasized more recently (145). All of these tracts are made up of fibers of varying length, some with one, others with two, still others with several cell stations interposed along the way. Return circuits are legion. Functionally, there is evidence that activity transmitted along these tracts does not result in further propagated neuronal action at the termination of the tract. Rather, graded changes in local potential, especially in dendritic networks, seem to result (52, 53). The changes produced by activity in the system are therefore changes in excitability rather than in the transmission of patterns of signals that convey large amounts of information.

Put together in this way, the data that have been reviewed here suggest that the limbic systems may be conceived to regulate the dispositions of the organism by interconnecting the various biased homeostatic mechanisms of the internal core of the brain stem. Interference with the limbic structures alters these dispositions. The biases of homeostats are set free of each other

and may become overly susceptible to change. Sequences of action that depend on the attainment of equilibration (i.e., completion of one unit of the sequence before the next is begun) suffer disruption. The animal cannot shift control from unit to unit because it cannot complete the test that meets the conditions of equilibrium in any one unit. There is either insensitivity to error or the mechanism that senses error continues to drift so that errors are registered irrespective of the situation (36, 37, 38). The patient with a limbic system lesion cannot order his sequences, cannot plan, if he cannot recall how he was disposed to do something. Memory for how one is supposed to do something is short-lived unless continually supported by external aids: the effect of cramming for an examination by rote memorization outlives the completion of the examination by a few days at best. A change in environment hastens the loss; in a few hours, or even minutes, the memorized material is inaccessible.

This analysis may, at this point, seem to be only a play on words, a bit of verbal magic. But as an hypothesis for further research it may nonetheless prove fruitful. A bit more precision in what is meant may come when the analysis is pursued in the discussion of the frontal intrinsic mechanisms.

In summary, then, the limbic systems are conceived to regulate the dispositions of organisms. The neural mechanisms by which dispositions are achieved are considered to be interconnections of units, each of which is a biased homeostat. Disturbed dispositions disorganize sequences of action by setting free the individual homeostats which then become overly susceptible to changes in bias. Sensitivity to increments in error is sacrificed, control cannot be shifted in an orderly manner from one unit to another of the sequence. The execution of sequences of actions, the execution of plans, is therefore disrupted. Patients cannot do something they are disposed to do; they can only memorize by rote how they are supposed to do it, so instructions have to be repeatedly available.

AN ALTERNATIVE TO THE CONCEPT OF CORTICAL ASSOCIATION AREAS

The conception of "cortical association areas" stems from two sources: Certain portions of the forebrain have obvious major direct connections with peripheral structures while others do not; the empiricist tradition holds that ideas are composed by the association of more elementary units, sensations. After a half century of experimentation, there is no direct evidence to support the notion that ideas are synthesized by association in those parts of the cerebral mantle that do not have obvious direct connections with the periphery. In fact, much of the evidence suggests a contrary view; viz., that the cerebral mechanism does not work by way of some simple transcortical reflex that transfers input from sensory areas to output via motor areas after integration has taken place in the association areas.

In the first place (119), there is direct input from the peripheral receptors, not only to the sensory receiving areas but also to the motor areas of the cortex. Furthermore, relatively direct outputs to muscles are known to

originate in all of the receiving areas. These outputs are independent of those that originate in the motor cortex. Second, when the sensory and motor areas are circumsected or thoroughly crosshatched, very little change in behavior, even in the most complex test situations, can be observed (30, 141, 150). Contrarily, undercutting of these areas produces profound disturbances of discrimination and skilled action. Input and output fibers, rather than transcortical fibers, appear to be the most important to these types of performances. Third, the data that relate the functions of the association areas to behavior cannot be easily fitted into an exclusively association strait jacket (119). For these reasons, the more neutral "intrinsic systems" is substituted here for the more common term "association areas." "Intrinsic" was originated by Rose & Woolsey (128) to make order in the rather chaotic classifications applied to the dorsal thalamus and its cortical projections. Their intrinsic thalamic nuclei receive no major extrathalamic, extratelencephalic input. There are two major divisions of the intrinsic systems: a posterior and a frontal.

The posterior intrinsic systems: an hierarchically organized representational process—reinforcement by cognition.—Analysis of the functions of the posterior intrinsic systems has proceeded at a rapid rate during the last decade or so. Much of this work has been done on rhesus monkeys; some, in the neurologic and neurosurgical clinics. A thorough review of these data was made by Rosvold in last year's *Annual Review of Psychology* (130). This discussion will, therefore, attempt to point out the major issues that have motivated the research, issues that are only partially resolved to date.

When a cerebral lesion impairs the functions of the posterior intrinsic systems, patients show a variety of symptoms and signs having certain similarities and also certain differences from those shown by patients with lesions that impair the functions of the classical projection systems. For the most part, impairment of function of the posterior intrinsic systems, when sufficiently restricted, is also related to one or another sensory mode. For this reason, as well as on the basis of anatomical grounds, the functions of the posterior intrinsic systems and those of the projection systems can be grouped together. Mode specificity is the common characteristic (119).

But the differences in the clinical picture presented by patients with lesions in the projection and in the intrinsic systems are equally impressive. Attempts to portray these differences are familiar—neurologists have spoken of "defective sensibility" and of "agnosia." Psychologists have been interested in teasing apart "existential discriminations" from "differential discriminations" (72) and "sensibility" from "intelligibility" (89, 102). These distinctions are made on the basis of whether the patient reacts to the simple presence or absence of a stimulus event or to some more complex relation between these events. Understanding the distinction appears, therefore, to hinge on comprehension of how organisms recognize stimuli.

We react to environmental patterns as if they are relatively stable configurations. Yet, because of movements made by the organism and changes

that take place in the environmental events, receptors are activated by ceaselessly altering patterns of energy. The constant or invariant properties of the proximal stimulus array must therefore be extracted somehow from these changing patterns. It is the function of the projection systems to accomplish the extraction. The details of the particular way in which this happens have recently been reviewed (153). Some precise guesses have been made in the form of mathematical models and by the simulation of simple neuronal networks in automata studies, and these will be reviewed subsequently. What is certain, however, is that the projection systems make it possible for an organism to respond to the invariant properties of receptor stimulation. For, as Klüver (81) has demonstrated so elegantly for vision, lesions of the projection systems lead to changes in behavior that can be described as follows: Ordinarily, an organism responds selectively to certain properties of the stimulus (e.g., contour, brightness). The range of transformations of these properties (e.g., changing a circle to an ellipse) over which the organism will still make the same response is relatively restricted. After ablations of the occipital cortex, monkeys will respond indiscriminately when the stimulus properties are transformed over a very wide range; only the amount of total luminous flux of the energy that activates the retina is now distinguished. Differences of flux that result in changes of luminance, contrast, and contour have no effect in altering the monkey's reaction. In the absence of the projection system mechanism, the organism cannot extract restricted invariant properties from the retinal excitation. It shows a defect in sensibility in making existential discriminations.

When the functions of the posterior intrinsic systems are interfered with, existential discriminations remain intact. A monkey with such a defect will catch a gnat in mid-air (17); he reacts to variations of illumination by varying his rate of response in an operant situation (43). But when he is given alternative responses to make to differences in luminance, pattern, etc. (the alternative indicated by a peanut, for example), he fails to make any consistent choice (27, 28, 29, 107, 110). It is apparent, however, that even this complex relation between cues, alternatives for response and the indicators of these alternatives allows some invariant properties to be extracted. Otherwise, intact monkeys and people would not be able to respond consistently. Somehow, through repetition in time, these properties are identified; and, when the functions of the posterior intrinsic systems are interfered with, identification goes awry. The situation becomes unintelligible to the organism; it cannot make the differential discrimination; it does not know what to do; it has an agnosia.

The posterior intrinsic system must, in some way or other, make possible the separation of the invariant properties that characterize the situation in contrast with other, less regular variables. This could be accomplished if some coded representation of the invariance is established in the posterior intrinsic mechanism. The neuronal patterns that form the representation can be conceived to be of the sort that Hebb (63, 64) has popularized as "cell

assemblies" with additional inhibitory properties such as those used by Milner in his Mark II modification (105). More in accord with the known complexities of the neural net, the neuronal patterns may be characterized in the manner suggested by Beurle (14), who bases his model on the cytological work of Sholl (137), and takes into account the graded response mechanisms emphasized earlier in this review. Beurle has worked out in some mathematical detail a mechanism of cortical function based on interacting waves of excitations or "interference patterns" that were first proposed by Lashley (86). However the representation is produced, it must be formed according to some rules established either by the innate structure of the nervous system or through experience. These rules proscribe constraints on the otherwise random properties of the neural network. The rules themselves, i.e., the properties of the network and therefore of the representation, are apparently modifiable, over time, by a variety of variables recurrent in the situation. However, the modification is selective, so that it must take place by some mechanism whereby the representation has efferent control over these variables (119, 120): by selective attention, in other words. What is selected could depend on some kind of match-mismatch process as described by MacKay (95) and by Bruner (21).

The selective process as it is detailed by these and other authors would provide the mechanism required by Harlow in his theory of discrimination learning (59). This mechanism also serves the purposes needed by the Gibsons (49, 51) to account for their findings that discrimination learning is a process of progressive differentiation, not a process of association. But perhaps the model has its greatest power in the description of what constitutes reinforcement for the organism. The posterior intrinsic mechanism, because of the hierarchical nature of its selective control over its own modification, allows a change in the representation to occur by trial and error. Whenever the error signal is such that the corrective change is not uniquely specified, the representation is modified to include this information, and trials continue. Thus an organism that possesses this mechanism can, given a relatively unchanging or slowly changing environment, search that environment for the additional information that is needed to make the organism fully informed. The neural model would thus account for the search through negative instances as these are defined in the stimulus-sampling type of stochastic learning theories (24, 41, 42, 56), search by an information-hungry organism reinforced or satisfied only when corrective change of the representation is immediate and can be deduced uniquely from the error signal. Stated in this way, reinforcement becomes one side of the coin of similarity! But more of this when the functions of the frontal intrinsic system are presented.

Techniques are already devised to test some of these notions directly. Microelectrode recordings made from cells located in the intrinsic systems show that the patterns of impulses they emit change as the animal learns to make a discrimination (74). Conversely, disruption of electrical activity

by mild electrical stimulation or by aluminum hydroxide cream applied to the intrinsic cortex interferes with discrimination learning, although performance of the same task remains intact under these conditions (114, 143). These and other preliminary behavioral data (116) suggest that this way of looking at the functions of the posterior intrinsic systems, though it may be wrong in detail, is a somewhat closer approximation to fact than the older theories based on the notion of the transcortical reflex.

The frontal intrinsic system: the association cortex for the limbic systems—intentions.—Views of the functions of the frontal intrinsic system have varied a good deal and, since the advent of psychosurgery, have usually gone to extremes. There are those who hold that the frontal cortex of man is the "organ of civilization" (58) and that tampering with this structure comes close to criminal action. On the other hand, there are those who claim that no consistent effects are ever observed to follow frontal lobectomy or leukotomy (99). What is the evidence?

Only a few standard psychological tests have been successful in demonstrating any change in the psychosurgical patient. The Porteus maze, the digit-span recall portions of intelligence tests, and nonsense-syllable recall seem most often impaired (134). Yet, psychiatrists and persons who are in close contact with a postlobotomy patient have no difficulty in spotting the fact that some important change has taken place in the patient. The manifestation of the change depends in part on the presurgical illness for which the patient was operated on; in part it depends on the premorbid personality of the patient. Obsessive and compulsive behavior is alleviated in many instances; chronic tensions and anxiety are relieved. All this at a price, and the price is so hard to define. Perhaps the difficulty lies in the approach to the problem. The change is not so much in what the person can or cannot do but in how he does it. Porteus maze, digit span, and interaction chronography (98a,b) are techniques that come closest to measuring "how" rather than "what," and thus they are the most sensitive to the changes produced by the psychosurgery.

A great deal of precise information about the effects of frontal intrinsic cortex lesions has been obtained from subhuman primates. These data have been extensively reviewed in these volumes from time to time, most recently, last year (130). Essentially, the story is this: In an attempt to show that animals, as well as people, have "ideas," Hunter (67) invented a simple task. Success depended on the organism's ability to recall some transient event that (a) changed from trial to trial, (b) characterized the situation at the time the task was set, but (c) had disappeared by the time response was allowed to occur. This delayed-reaction task and some other similar tasks that were derived from it (e.g., the delayed alteration, the double alteration, etc.) were found by Jacobsen and his collaborators (70, 71) to be sensitive and selective indices of the functional integrity of the frontal intrinsic cortex of subhuman primates. The question remained to be answered as to just what was the nature of the "ideas" that the tasks were presumed to test

for, and just what could be the neural mechanism that mediated them. During the past two decades, a considerable amount of data has accumulated and these data do suggest some explanations.

The problem of frontal lobe function is thus seen to be somewhat similar to that faced in the discussion of the functions of the limbic systems. Two sets of data appear, on superficial examination, to be irreconcilable. The data obtained with "limbic" patients and "frontal" animals point to a memory defect; the data obtained with "limbic" animals and "frontal" patients point primarily to defective emotional-motivational processes. In the discussion of the limbic systems, reconciliation was effected when both types of change were considered to be due to failures on the part of the damaged organism to carry out complex sequences of action. Perhaps this approach will serve as well for the discussion of the functions of the frontal cortex.

First, in contrast to the effects of posterior intrinsic system lesions, the effects of frontal lesions are nonspecific with respect to sensory modality. There is an abundance of anatomical and physiological evidence that the frontal intrinsic system is closely connected with the nonmodality-specific systems of the internal core of the brain stem and the related limbic formations of the endbrain. This evidence is reviewed in detail in a recent publication (117) and so does not need to be recapitulated here. In short, the frontal intrinsic system can be conceived as the "association cortex" for the limbic systems. And these, as already noted, deal with the dispositions of the organism that are necessary to maintain sufficient stability to allow the execution of complex sequences of action.

Second, data have accumulated to show that frontal lesions interfere with whatever occurs at the time the delay task is set in the delayed reaction type of experiment, not with the process of recall (at the time response is allowed) per se (108, 109, 123). Thus, the frontal lesion appears to interfere with the monkey's ability to be instructed as to how to behave in a subsequent portion of the situation. The lesioned monkey is not able to perform as he is supposed to perform unless the instructions are present in the environment at the time a response is required. He cannot recall an instruction that, to him, did not instruct. The defect appears to be less that of "immediate memory" than that of confusion of intention, i.e., of how sequences of actions are to be executed. This confusion seems to be due to an inability to arrange and utilize the information given by the task in the absence of persistent and detailed external instructions.

Stated in this way, the defect that follows frontal lobe lesions in primates might be attributed to a defective representation of intentions. The frontal representations can be conceived to have properties similar to those described for the representational process of the posterior intrinsic systems. The representation is based on some more or less random network of neurons constrained by rules that are partly determined by the nature of the network and partly by experience. The experience that modifies the representation is selected: the representation, by a hierarchically organized match-mismatch

process, efferently controls the mechanism that determines error. But what will serve as an error signal for the process differs in origin for the frontal and for the posterior systems. Because of its connections with the projection systems, the posterior intrinsic mechanism is sensitive to differences between past and present constancies in receptor stimulation. The frontal intrinsic mechanism, on the other hand, by virtue of its connections with the limbic systems, is sensitive to differences between past and present constancies in the dispositional states of the organism. An error signal would be instituted whenever the representation of past perturbations of the ultrastable dispositions of the organism did not match present perturbations. The hierarchical organization of the process would allow change in the representation to occur by trial and error: the modification would be selectively controlled by the representation. Whenever the error signal is such that corrective change is not uniquely specified, the representation is modified to include this information, and trials continue. Thus an organism that possesses this mechanism can, given relatively unchanging or slowly changing conditions, search those conditions for the additional instructions that are needed to make it fully instructed. The organism would be reinforced only when corrective change of the representation could be deduced uniquely from the error signal, i.e., when further change in the representation is precluded. Stated in another way, the organism is "gratified" only when he can do things pretty much as he intends to do them. Given the frontal mechanism, his intentions can be uniquely gratified in any particular set of circumstances. In the absence of the frontal representational mechanism, gratification, i.e., reinforcement, would result from a greater variety of conditions; thus "trials" would cease to be trials that provide instructions.

The subhuman primate, and even man, is relatively limited in the capacity to be instructed without the aid of external crutches such as written words, mathematical tables, and pencil and paper figuring. The delayed-reaction situation is at the limit of the capacity of subhuman primates; digit-span recall, when distraction intervenes, appears to be close to the limit of human performance. Try to recite two series of seven random digits, each presented only once and the second presented before an opportunity for recitation of the first is given. Even the "organ of civilization" isn't good enough for that one.

In summary, then, the frontal intrinsic mechanism shares characteristics with the posterior intrinsic systems. Both are conceived as the locus of representations sensitive to, but not exclusively determined by, experience. The intrinsic representative process is based on neural network which is constrained by some innate properties (such as inhibitory mechanisms, graded response characteristics, and differences in interconnections and, therefore, in the timing of firing patterns) and by the effects of experience. However, the experience that modifies the representation is only partly determined by circumstance. Equally important is the selection of the experience, on the basis of the representation, the selection accomplished by an efferent mech-

anism that originates in the intrinsic systems. The intrinsic representational process is thus hierarchically organized. It is altered only by what it allows itself to be altered by. It is sensitive to variations in circumstance, provided that these variations are not overly abrupt.

The differences in function between the frontal and the posterior intrinsic mechanisms stem from differences of their connections. The posterior systems are primarily related to major projection systems that are organized to select the invariant properties of receptor stimulation. The frontal mechanism is primarily related to the limbic formations of the endbrain that are organized to enhance constancies of state that depend on the biased homeostats of the brain-stem core. The posterior intrinsic mechanism, therefore, is sensitive to differences between current and past receptor-stimulation; the frontal intrinsic mechanism is sensitive to differences between current and past perturbations of states of the organism. By virtue of its *posterior* intrinsic mechanism, the organism is reinforced or satisfied only when it is fully informed, i.e., when corrective change of the representation is uniquely specified by current receptor stimulation. Search for information continues until this condition is met. By virtue of its *frontal* intrinsic mechanism, the organism is reinforced or gratified only when it is fully instructed, i.e., when corrective change of this representation is uniquely specified by current perturbations of organismic states. Attention to instructions continues until this condition is met. Reinforcement conceived as satisfaction turns out to be the identification of similarities; reinforcement as gratification, the fulfillment of intentions. A somewhat different view than that derived from S-R reflexology and classical associationism!

SITUATIONAL DETERMINANTS

No discussion of functional localization within the central nervous system is complete without some mention of the troublesome problem of what is localized. Most of the objections against localization have been raised because it is deemed logically inadmissible to localize mental functions in the physical brain. Parallelism, reductionism, and phenomenal or physicalistic monism have all been invented to surmount this issue. Another course can be taken (118). Different parts of the brain are shown to have different functions: The frontal lobes and the occipital cortex regulate different aspects of the organism's behavior. But these different functions are not to be the loci of some simple psychological process inferred directly from the observed behavior. Rather, the brain process is shown to be a critical determinant of the behavior under certain conditions (121). Only when these conditions are thoroughly explored can the brain process be adequately specified. Specification is, as a rule, in terms somewhat different from those derived exclusively from the observations of behavior that initially instigated the localization research. The brain processes, in other words, constitute only one, albeit often a critical one, of the several classes of variables that determine the organization of behavior. Brain processes and psychological processes are

thus not identical, nor parallel. Psychological processes represent a different and more complex level of discourse. Thus, the psychological process is characterized by properties unique to this level of organization. Specification of the properties of the component elements of this organization, while a proper pursuit of science in its own right, must not be confused with the search for specification of all of the properties of the more complex organization. The aim of neuropsychology, i.e., to specify brain processes that critically determine the organization of behavior, is thus seen to be a limited one. An example may serve to illustrate some of the steps that can be taken to realize this limited aim.

Resection of the amygdaloid complex of the limbic systems of the end-brain results in a syndrome (discussed earlier in this review) that includes, in several species, extreme taming and hypersexuality (82). A series of experiments undertaken to quantify the taming (fleeing and fighting) by measuring the reactions of monkeys in a social dominance hierarchy disclosed that taming is not always produced (131). In fact, whenever the number two animal in the hierarchy is fairly unreactive and the dominant monkey is the one operated on, then the operated monkey remains dominant and may indeed become even more aggressive than he had been before operation. A similar result is obtained when pairs of animals are tested against each other or when operated monkeys are handled in several different ways by their keepers after surgery (152). Amygdalotomy, therefore, does not necessarily produce taming: the amygdala is not the "seat of aggressivity." Rather, as Weiskrantz has suggested, amygdalotomy can be conceived as an interference with a mechanism that relates the momentary social behavior of the monkey to its prior behavior. In this situation, as in others such as food-rewarded operant-conditioning experiments, the amygdaloid mechanism can thus be tentatively but usefully conceptualized, as Schwartzbaum (135) has done, as a governor of generalization based on experience.

Support for this view of the functions of the amygdaloid region comes from careful study of the effects of amygdalotomy on sexual behavior. Hypersexuality was the immediately obvious effect (133). Hormone studies, etc., were undertaken, only to give equivocal results. But control of the situation (57a) in which the hypersexuality was seen to occur, and comparison with the range of normal animals' sexual behavior, made it clear that cats, at least, behave sexually in much the same way whether they possess their amygdaloid complex or not. However, the occasions on which, and the territory in which, they display sexual behavior are markedly affected by amygdalotomy. Normal cats restrict their sexual activities to their own territory and to their own species, types of mates and situations thoroughly explored and delimited through prior experience. Cats devoid of their amygdaloid region, on the other hand, suffer no such restrictions; they behave according to their momentary dispositions without regard to other factors. But, even in this context, the effects of lesions are not always totally disruptive. Certainly, then, the amygdala cannot be conceived as

some simple "sex center." The more appropriate view is attained only after careful exploration of the situational determinants of the behavior that is studied: in these situations, as in those in which dominance was studied, the amygdaloid mechanism can be tentatively thought to govern generalization based on experience.

The amygdaloid complex is one of the formations of the limbic systems of the endbrain. Already reviewed are the data demonstrating that these formations make possible the execution of complex sequences of action. The anatomical and physiological evidence suggests, as was detailed earlier, that the limbic formations organize the biased homeostats of the central core of the brain stem into an ultrastable multilinked mechanism sensitive to events that result in changes of the excitability of the system. The experiments on dominance and on sexual behavior suggest that the amygdaloid region is involved in these functions as a mechanism that allows current changes in excitability due to social and sexual stimulation to be constrained by the effects of past experience and, perhaps, by other classes of variables such as the total situation, nonsocial and nonsexual excitations (e.g., hunger), etc. The effect of the lesions in the amygdaloid region on the execution of the sequences of action necessary to dominance and mating is therefore not to be conceived as some change in the response mechanism *per se*; rather, the change is in some properties of the antecedents that determine the behavior. The range over which these antecedents are changed is a matter for laboratory test. Preliminary experiments suggest that generalization as tested in a transposition situation is as affected by amygdectomy as is generalization in a social and sexual situation (135a). Thus, the function of the amygdaloid complex is characterized as a mechanism involved in stimulus generalization or stimulus comparison which may or may not be especially limited to this or that situation. Should it turn out, as is beginning to appear, that the mechanism is important in a wide variety of situations, then the problem arises as to how it is that a defect in the mechanism affects especially the execution of complex sequences of actions. In other words, how do the dispositions of the organism determine the generalization process? Thus, by progressive approximation, questions are asked that are at the same time more specific in neurophysiological and neurobehavioral detail and more general in their application to a wide variety of problems of psychological function. Such a step-by-step analysis, by providing concepts of mechanism at several levels, seems to steer clear of metaphysical difficulties.

SIMULATED BRAINS, COMPUTERS, AND AUTOMATA

The picture of the central nervous system to which our theory leads is a picture of a more complex and active system than that contemplated by most associationists. The notions of "trace," "fixation," "excitation" and "inhibition" suggest a relatively passive electrochemical system (or, alternatively, a passive "switchboard") acted upon by stimuli, altered by that action, and subsequently behaving in a modified manner when later stimuli impinge on it. In contrast, we postulate an information processing system with large storage capacity that holds, among other things, com-

plex strategies (programs) that may be evoked by stimuli. The stimulus determines what strategy will be evoked; the content of these strategies is already largely determined by the previous experience of the system. The ability of the system to respond in complex and highly selective ways to simple stimuli is a consequence of this storage of programs and this "active" response to stimuli (113).

The author of the present review came across this passage, so closely paralleling his own thinking, during his readings preparatory to the composition of this last section. The article from which the above quotation is taken was not written by physiological psychologists in the classical sense of the term. In fact, the men responsible for these ideas might well need resuscitation were they to experience the travails of the neurosurgical or neurophysiological operating procedure. Their *métier* is made of pencil and paper, of solder and magnetic tape, not of Wisconsin and Operant boxes, not of primate bone and brain. Yet their contribution to the subject matter of physiological psychology—and that of many others who work with similar tools—can be ignored by their bloodier colleagues only at a price. Mathematical and metal models of brains can teach much. In fact, they have already taught much to those whose intense interest has surmounted the obstacles posed by mastery of three separate disciplines: physiology, psychology, and communications and control engineering. The problems faced are similar in all three areas: What are the component elements of nervous systems and computers and how are they organized into functional systems? How do automata or organisms control their own behavior? What kinds of mechanisms do we need to explain this or that psychological phenomenon? The last section of this review is not written with any sense of competence in communications and control engineering; nonetheless, the matter is sufficiently important to warrant the attempt to bring together in one place all three domains of neuropsychology.

BASIC MECHANISMS

Components.—The components of simulated brains are of two sorts: digital and analogue. The digital components serve functions that were discussed earlier as all-or-none; the analogue mechanisms are akin to the graded response processes emphasized recently in the study of animal and human brains. Digital elements are characterized by the fact that they can exist in only one of a discrete number (usually small) of states. Thus a wall switch that controls the ceiling light is a digital mechanism. Analogue elements are characterized by the fact that they can be in one of a continuously variable series of states. The volume control of a radio is an example of such an element. For the most part, computers have been developed from digital elements; automata from analogue elements. But whenever the behavior that the mechanism is to simulate is at all complicated, combinations of the two sorts of components are necessary.

Simple automata.—The best known automata are Walter's turtle (151) and Ashby's "homeostat" (7). The turtle can respond to two types of input:

light intensity and touch. It moves about, and can escape from enclosures and the like. Additional circuitry allows it to learn. This circuitry is essentially a memory of the resonating (feedback) type and makes the turtle extremely sensitive to repeated transients that are within the frequency range to which the circuit is tuned. As Walter puts it, this "sensitivity to rhythmic stimuli would be a serious fault in a tool machine but is a virtue in lifelike toy, for it exists in animals." Some insight into the "theory of learning and the temperaments (dispositions) of the learners" can be gained from the settings that have to be made in order to allow the model to perform as "sensibly" as would a "good" animal.

The problem of equilibration is faced in the turtle; it is tackled more specifically in the design of the homeostat. This design is a complex of simple servos of the nature of the TOTE units discussed earlier. The units are interconnected by feedback loops so arranged as to provide initially a somewhat chaotic system. Each unit then acts on the others to enforce changes in the system as a whole that will bring it to some stable state. Any perturbation of the system, irrespective of how produced, will be temporary; the system will again interact until the stable state is attained. The system has been characterized as being ultrastable and as showing a disposition to attain the particular state toward which it is always restored. Again, some additional feedback memory circuitry can be developed to modify the mechanism so that it can select its dispositions: thus problem solving, as a process of selection of information, is accomplished (8). This is only one of many specific suggestions made to this end; others are described in the following section.

MATHEMATICAL AND METAL MODELS OF PSYCHOLOGICAL PROCESSES

Representation, recognition, and cognition.—Patterns can be selectively reacted to by machines that are devoid of feedback loops. The essential organization is one of convergence and divergence in a random net of connections of the elements. Early attempts produced devices of very limited capacity. Only the presence or absence of some predetermined environmental event was effective in altering the response of the system, much as was the case with the turtle. For more complex systems the simple convergence-divergence property of the mechanism had to be modified. Two types of modification have been made. The first includes inhibitory as well as excitatory processes. Milner (105) has modified Hebb's cell-assembly structure (63) to this effect. This modification was found to be necessary when Gelernter & Rochester (46, 127a) attempted to build a metal model of Hebb's "conceptual nervous system" and found that it learned much too much ever too fast. Mark II with its inhibitory circuitry gets around this.

The other way in which the problem has been solved is to put into the system some method of time delay between the arrival or activation of various signals generated by any particular input. McCulloch & Pitts' ascansion device is of this nature (96). Uttley's method for sensing patterns with a conditional probability machine is another example (148, 149).

Licklider's model of the auditory mechanism as an autocorrelation computer is yet another (89).

All of these systems are based on the assumption of a random network of interconnected elements. The signal passes through the network on a probabilistic basis. Thus, it is stochastically determined whether or not any particular element is activated. Any method that biases the probability of reaction of any of the units therefore limits the initially random nature of the net. Inhibitory mechanisms, scansions, and time delays produce such biases and therefore constrain the system. The constrained system reacts differently from the free one; the amount of constraint can be predetermined (e.g., by nonrandom connections of neural or computer elements) or it can vary as a function of successive inputs, etc. (80, 106).

The above models have the virtue that they can react immediately to certain stimulus patterns and that there is flexibility with respect to which patterns a particular machine can react to at any particular time. But in order to behave selectively on the basis of the representation, additional circuits are required; and, as in the case of simple automata, these circuits are recursive, i.e., they have the special property of a feedback that modifies subsequent activity in the system and is, in turn, modified by the modification. This property allows the machine to match the current input with some representational process. The representation may be built into the model or set up by prior inputs or be the resultant of the interaction of both (80). The representational process can be a purely topological one; in that case, the representation is some sort of filtrate of the input (19). More interesting are the situations in which the representation is formed by a set of rules which describe the constraints on the system. These representations are thus coded transformations of that which they represent. The code or rule does not need, therefore, to resemble the input pattern. Match is determined by fit to the rule, not by some qualitative correspondence. The variety of rules that can accomplish this effect is legion. Some examples show the range over which these devices can operate.

When the rules that are the representation comprise coded transformations of the physical parameters of the input, perceptual phenomena may be reproduced by machine (129). The computer may be programmed with various geometrical transformations that have been shown to operate on optical arrays to produce the standard visual phenomena that guide our behavior. The experiments performed by Gibson (50) and those of the Ames group (5) have detailed some of these rules; when these are used as programs, complex visual displays can be synthesized from relatively simple elementary inputs.

MacKay, to whom this review is repeatedly indebted, has taken the problem one step further (95). He makes the interconnections between elements of a system function probabilistically. Specifically, this produces a mechanism in which the probability of excitation of each element can be made to depend on continuously variable physical factors as well as on the

current states of any one of the other elements linked to it, as in the simple automata described by Ashby and Walter. In other words, graded response mechanisms are posited to influence not only each element but also the relations between them. A system is then arranged so that the incoming signals stimulate the representation and in this way set it to adapt and match or counterbalance the signal by its internal activity. By continually modifying its activity (according to some rule) to match the incoming signals, the mechanism may be thought of as hierarchical: i.e., as symbolizing those features of the received information that have necessitated the modifications. MacKay states:

The symbol generated in this way must remain the same under all transformations of the input with respect to which the rule or "concept" is invariant. The internal activity evoked in the matching-response to the incoming signals is outward directed; and it is the outward-directed activity of the elements organizing the internal matching-response, that constitutes the basic symbols that now make up the concept. Selection is accomplished not by filtration but by an active searching process. Error is recognized.

Shades of the workings of the intrinsic mechanisms of the brain as these were described on pages earlier

Logic.—MacKay calls his machine an epistemological automaton. He leaves somewhat vague the nature of how the rules are formed that guide his machine to modify the representational activity to match the input. But rule formation has also been tackled by theoreticians familiar with simulated brains. Von Neumann (112), for example, discusses the synthesis of reliable organisms from unreliable components and comes up with a method for the study of a probabilistic logic. Carrying on from the fundamental work of McCulloch & Pitts (96), von Neumann details the types of elements, their connections, and the results that can be obtained from several of the possible networks. He uses inhibitory as well as excitatory circuits; he does not, however, deal with the effects that graded response mechanisms might have on these systems.

A still different approach to the simulation of logical processes is taken by those who have been primarily concerned with the programming of existing computers. An outstanding contribution to this approach comes from Newell, Shaw & Simon (113). The authors talk about computers whose components are of the von Neumann type, and of problem-solving organisms as information processing devices. Information processing is programmed. Programs are made of lists of elements. Elements consist of an item, the address (identification number) of that item, and an address of some other (predetermined) item. Elements are stored in a memory and are made available to computation when their address appears on the initial list that is fed into the computer. Thus a hierarchy of lists constitutes the "information processing language." A special device, an interpretive routine, has to keep track of where, in any particular list, the process has shifted to a sublist. Without

this routine the computer would stop after it had exhausted the items on the sublist.

The model of problem solving that is provided by their logic theorist is startling in its similarity to the neuropsychological model developed in the body of this review. The latter is based on neurophysiological and neurobehavioral data (116, 120) and on mathematical models, especially the American statistical learning theories (24, 41, 42, 56) and the British simulation and automata studies (7, 8, 14, 19, 36, 37, 38, 95, 137, 148, 149, 153). The logic theorist, on the other hand, was derived almost wholly by programming computers. Another quotation from the paper by Newell, Shaw & Simon (113) shows the extent of congruence that has resulted:

Problem solving is said to involve (a) finding means of solution, and (b) applying them. A counterpart in the logic theorist is the division between the similarity routines which find "likely" materials for a proof, and the matching routines, which try to use these materials. In applying means (matching routines), there are needed both *ordering* processes (to assign priorities when more than one method is available) and *control* processes (to evaluate the application).

Newell, Shaw & Simon's "similarity routines" correspond to neurobehavioral theory when reinforcement (as a function of the posterior intrinsic mechanism) is conceived as the identification of similarities. Their "matching routines" correspond to the neurobehaviorally derived statement that the defect that follows frontal lesions in primates appears to be "less that of immediate memory than that of confusion of intention—i.e., of how sequences of actions are to be executed. This confusion seems to be the result of an inability to arrange and utilize the information given by the task." "The ordering processes (to assign priorities when there is more than one method available)" of the logic theorist correspond to the neurobehavioral process described as "the defect that follows frontal lobe lesions in primates—attributed to a defective representation of intentions." And to push the analogy to the extreme: the computer's "control processes (to evaluate the application)" could correspond to the neural mechanism involved when the animal with limbic lesions "cannot shift control from unit to unit because it cannot complete the test that meets the conditions of equilibrium in any one unit—there is insensitivity to error, or, the mechanism that senses error continues to drift so that errors are registered irrespective of the situation." Such convergence in detail of completely independent theory constructions suggests that perhaps at last neuropsychologists have seized some psychological truths by the tail.

RECAPITULATION

A great deal of ground has been covered. Theorists have not been idle in physiological psychology—though, until very recently, their efforts have been overshadowed by those of the data gatherers. Some illuminating threads run through the various arguments and these have been followed, pulled out,

and used to weave a cloth from the strands of data that have accumulated. A consistent view of the regulation of behavior by the nervous system has resulted, and forms the substance of this review. In conclusion, these threads may profitably be identified as they appear in their new matrix.

a. An hierarchically organized representational process is conceived as necessary and sufficient to account for reinforcement. The build-up of a representation in metal or neural systems has long been recognized as an important mechanism if the facts of a behavioral psychology were to be dealt with. Lashley (86), Hebb (63), and Broadbent (19), especially, have recently spelled out the implications for physiological psychology that such representational processes provide. As exemplified in the work reviewed, a great deal has been done with the problem of how the representation is constructed and how it may operate. But the importance of the hierarchical nature of the organization that is necessary if the representation is to do the work that it must for psychology was largely ignored until MacKay (95) focused attention on the problem. The hierarchical organization of the representational process makes it possible for the representation to be modified selectively. The selection, in turn, depends on the representation, so that in an unchanging or gradually changing situation the representation can achieve a unique match with the situation. This possibility provides the key to the puzzle of what is reinforcing to an organism. Only when unique match is achieved will the organism stop search. Only then will it come to asymptote in learning. Only then will the probability be maximized that a particular response alternative is chosen.

b. Two kinds of reinforcing mechanisms were distinguished. Two sorts of programs are necessary to allow a computer to solve problems: programs that gather information and programs that order and utilize the information that has been gathered. The brain also has two major programming devices, the posterior and the frontal intrinsic systems. The posterior, by virtue of its connections with the classical projection areas, is sensitive to differences between past and present invariances in receptor stimulation. It is thus suited to aid the organism's search for information. Because of the hierarchical nature of the representational process, search for information in any particular situation proceeds until the organism is fully informed in that situation, i.e., until he has complete knowledge. Only then is he satisfied. The frontal mechanism works in similar manner, but, by virtue of its connections with the limbic systems, this mechanism is sensitive to differences between past and present perturbations of the dispositional states of the organism. As a result of the operation of this mechanism, the organism remains active until it is fully instructed, i.e., until it has the know-how to arrange and utilize information. Only then is it gratified. By the use of their intrinsic systems, organisms are thus able to display both knowledge and wisdom.

c. Ultrastable dispositional states are accomplished for automata and for flesh and blood organisms by multilinking several homeostatic units. This organization is performed for the organism by the functions and connections

of the limbic systems of the endbrain. These systems were conceived to control the biases of the homeostats of the central core of the brain stem and thus make possible the ordering of behavioral processes—the execution of sequences of action. Lesions of the limbic systems disjoin the homeostats and set them free so that small changes in conditions no longer register as errors. The biases of the homeostats become overly susceptible to the change. The equilibratory mechanism is thus easily thrown into oscillation. Or the bias may drift so that error is registered irrespective of the situation. As a result, the organism cannot test to determine whether any element in a sequence has been completed. Thus, the limbic mechanisms of the endbrain are conceived to control the dispositions of the organism: the reported effects that lesions have on the memory process and on motivation and emotion are thought to be secondary to disturbances of dispositional states.

d. The theory of homeostasis is based on the fact that equilibratory regulation of a function is accomplished through a mechanism whose sensitivity controls that to which it is sensitive. Homeostats abound in the internal core of the brain stem. But, recently, an adjacent mechanism has been discovered: the modality nonspecific activating systems. Data obtained from stimulations and destructions of these systems have been interpreted to support directional theories of drive. Directional theories are of three types: generalized activation, specific sensory, and hedonistic (pain and pleasure). These may all be more or less apposed to equilibrational or optimal state notions. None of these ways of looking at the mechanism of drive is satisfactory since none of them subsumes a large enough body of the data that are covered by the other theories. A somewhat more adequate picture has been obtained upon consideration of the complete mechanism of the homeostat. Homeostats such as the thermostat can be tuned or set; they are subject to bias. The activating mechanisms, adjacent to the core homeostats, function primarily as graded response mechanisms. Changes in their excitability can be conceived to alter the biases of the homeostatic mechanisms that they surround. Biased homeostats can function either in an equilibrational or a directional fashion, or they may oscillate. When biases are set, equilibration results from the operation of the homeostat. When biases are shifted slowly, the homeostat adjusts and direction is achieved. When biases are altered rapidly, marked oscillations can ensue. Drive, as regulated by biased homeostats, is therefore neither purely directional, purely equilibrational, nor purely hedonistic.

e. Until the past few years neural function was conceived primarily in terms of impulsive activity, or signal transmission. Now it is recognized that changes in excitability, or graded responses of neural tissue, are as important to an understanding of function as is the transmission of impulses. The all-or-none law has been modified in favor of an all-or-something law. Graded responses are characteristic of fine fibers, especially dendrites, and of synapses. They are thus the prepotent mechanisms in such locations as the nonspecific systems of the brain-stem core and the dendritic layers of the

cerebral cortex. Graded responses can account for phenomena that are not accounted for when the nervous system is conceived entirely in terms of signal transmission. The biasing of homeostatic control of drives is one example. Köhler's (83) explanations of the mechanism of some perceptual phenomena and Lashley's (86) and Beurle's (14) conceptions of cortical function in terms of interference patterns are others that today seem not at all farfetched.

f. The homeostat is an example of a unit of organization of the nervous system and of behavior that may have to replace the S-R reflex-arc concept. The reflex arc must, in the light of the new data, be modified to include efferent control of the receptor element of the arc. This modified unit is a simple servomechanism. Complication of the unit of analysis requires a review of some notions that are held about what constitutes a stimulus for an organism and for what reason the organism responds. The suggestion is made that a sequence of functions describes the way in which servos work. There is a test phase in which a congruity or incongruity between the state of the test unit (e.g., the receptor) and an input to it is sensed. Incongruity shifts control from the test phase to an operate phase during which process the organism and the environment are changed until the input to the test is congruous. Then, and only then, are the conditions satisfied that allow transfer of control to other units, i.e., exit from the servo. This Test-Operate-Test-Exit (TOTE) unit places emphasis on an active organism that controls the stimuli to which it is sensitive and upon which it acts. This conception differs from an S-R reflex-arc concept in which a passive organism is completely subject to the exigencies of its environment.

g. This view of an active organism gains support from the fact that the central nervous system, in conjunction with its receptors, is intrinsically and spontaneously active. Electrical activity is recorded in the total absence of environmental input. Even brief stimulation has long-lasting aftereffects that alter the intrinsic rhythms for hours and days and thus change the response of the organism to subsequent stimulation.

Reinforcement by cognition, based on a mechanism of hierarchically organized representations; dispositions and drives regulated by multilinked and biased homeostats; representational organization by virtue of graded, as well as all-or-nothing, neural responses; spontaneously generated, long-lasting intrinsic neural rhythms; organisms thus conceived are actively engaged, not only in the manipulation of artifacts, but in the organization of their perceptions, satisfactions, and gratifications.

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As this review is going to press, Professor A. Luria comments in response to a preview, "Too bad you all do not use Russian literature!" He suggests especially articles in the journal *Questions of Psychology* and: (a) On feedback, A. D. Beznstein, "Problems of Co-ordination and Localization," *Arch. Biol. Sci.*, 38, N7, 1955, and *On the Construction of Movements* (Med. Press Publishing House, Moscow, 1947). (b) On reinforcement, P. K. Anokhin's mechanisms of an "action acceptor," *Problems of the Center and the Periphery in Physiology of the Nervous System* (Gorki State Publishing House, 1935); *Problems of Higher Nervous Activity* (Acad. Med. Sci. Publishing House, Moscow, 1958); Inner Inhibition as a Physiological Problem (Med. Press Publishing House, Moscow, 1958). (c) On disposition, D. N. Usnadze, *Experimental Investigations of Set* (Review of 25 years of work).