TRENDS IN THE DEVELOPMENT OF PHYSIOLOGY OF THE BRAIN

BY

JERZY KONORSKI

Reprinted from

THE JOURNAL OF MENTAL SCIENCE

Vol. 104, No. 437, October 1958

TRENDS IN THE DEVELOPMENT OF PHYSIOLOGY OF THE BRAIN*

By

JERZY KONORSKI, M.D.

Head of the Department of Neurophysiology of the Nencki Institute of Experimental Biology in Warsaw, Poland

INTRODUCTION

THERE is hardly any field of natural science where development is so erratic as that of the physiology of the brain. It is true that perhaps no branch of science develops quite evenly. Very often the domination of old and deeply-rooted theories is so strong that they cannot easily be removed under the pressure of new facts, and consequently they may hamper the progress of science in the given field for many years. But generally the development of natural science is straightforward in the sense that its every stage is a logical consequence of the previous stages, and that particular lines of investigation tend to complement each other and eventually to merge into a single whole.

Unfortunately nothing of this kind is seen at present in the field of the physiology of the brain. This vast and extensive province of neurophysiology, the primary importance of which lies in the fact that the brain "governs" the behaviour of an animal as a whole, has presented up to now a huge assembly of mutually unrelated groups of data, and an aggregation of independent and often contradictory theories. While in other fields of science all specialists use the same language and therefore can always understand each other, the physiology of the brain reminds us of the biblical tower of Babel whose architects had their tongues "confused" and one and the same word took on quite different meanings.

This situation is explained by a number of factors, of which two, perhaps the most important, will be dealt with first as being of a most general and essential character.

First, however, it should be noticed that in every field of science there emerges in the course of progress a definite model of the phenomena concerned, a model enabling its students to systematize the facts they discover, to interpret them, and to set the course of further work. With the progress of research, the model itself, of course, changes quite considerably: it becomes enriched by new details, or is modified, or complicated, or in some rare instances, it is completely abolished and supplanted by a new one. But in the absence of such a model the given branch of science fails to develop into an organized scientific system and remains merely a store of accidental unrelated observations forming no integrated entity.

To give some examples. The model which guided the development of chemistry in the nineteenth and the beginning of the twentieth centuries was the atomic theory supplemented by the theory of valencies, now deepened and enriched by the concepts of atomic structure. The model in modern genetics is the concept of genes. In the physiology of blood circulation, a model has been

* The subject of a lecture delivered in Cambridge on 12 November 1957.

supplied by Harvey's discovery of the "motions of the heart", enriched later by the mechanics of capillaries and in recent years by demonstration of arteriovenous connections. In the physiology of the spinal cord a model has been afforded by the concept of the reflex arc, more recently deepened and generalized by the principles of neuron organization (see below).

The first factor responsible for the inadequate development of the physiology of the brain is that physiologists have failed to produce a satisfactory and generally accepted model of the function of this organ. When Pavlov, investigating the physiology of higher nervous activity, established the concept of the conditioned reflex, it might have appeared that a road leading toward systematic and orderly study of cerebral functions had been opened. It seemed that, in the same way that the concept of the spinal reflex had become a guiding principle in research on lower functions of the nervous system, so would the conditioned reflex become with regard to the higher functions. Indeed, the first years of research in this field, guided by the idea of the conditioned reflex, proved to be remarkably fertile. But then disappointment followed. First of all, Pavlov himself did not adhere to the idea with absolute faith. The reason was undoubtedly the fact that the behaviour of animals and man, as can be seen in everyday life and even in the most simplified experimental conditions, is so complicated that its conditioned-reflex composition is by no means so evident as is the unconditioned-reflex composition of spinal activity. Pavlov, therefore, was compelled to extend the concept of the conditioned reflex so much that it became tantamount to the concept of association, well known in psychology. Then, by introducing the concepts of irradiation and concentration of excitation and inhibition and their mutual induction (with which we shall deal later on) Pavlov receded even further from his original conception, as he accepted the existence of cortical processes overtly distinct from those of conditioned reflexes. The conditioned reflex concept also came up against criticisms from numerous scientists outside the Pavlovian school: some queried whether conditioned reflexes are really *elementary* phenomena of cortical activity, while others doubted whether the *entire* cortical activity could be thereby elucidated.

Be that as it may, it must be realized that the brain of the higher animals, and especially the cerebral cortex, is for us at present, as far as its activity is concerned, the most mysterious and incomprehensible of all organs of the body. How very limited, fragmentary, and even possibly erroneous, is our knowledge about it is best recognized by those who are directly concerned with its study. This was perfectly understood and felt by Pavlov himself when he wrote the significant words: "In this realm of science, the mountain of the unknown will for a long time tower above the tiny fragments of the known."

The second important factor is that the functioning of the brain is connected in some way with psychological phenomena, known to each of us from introspection and being the subject of a discipline far older than physiology, namely of psychology. Since the behaviour of animals and man can be considered as a manifestation of cerebral processes as well as psychological phenomena it is clear that much the same territory is explored both by physiologists and by psychologists. This fact not only does not help in the exploration of this territory, but on the contrary creates even greater confusion, since both groups of scientists are to some extent antagonistic to each other: and many psychologists believe either that physiology is not competent at all to deal with animal behaviour, or else that it is not yet sufficiently "grown up" to engage in such studies.

On the other hand, psychologists themselves are very much in conflict about the scope and purpose of their research and the evaluation of the phenomena with which they deal. The fact that there are so many names denoting one and the same subject of investigation (zoopsychology, behaviourism, physiological psychology, ethology, neuropsychology, etc.) shows how great a confusion reigns at present among various psychological schools, and that even the psychologists themselves have not found a uniform language.

Lastly, we must remember that on the other side of the territory held by the physiology of higher nervous activity there extends a vast field of research explored by electro-physiological methods, and again between these two fields of investigation there is no close relation.

When all these factors are taken into account one can understand to what extent the physiology of the brain represents nowadays an incoherent tangle of disconnected threads and how particular scientific centres not only fail to support one another but remain in relative isolation or antagonism and frequently have no means of communication at all.

This paper is intended to give a brief description of various trends of the cerebral physiology and to comment on the prospects of further progress, and on the possibilities of rescuing this branch of science from its present state of confusion.

The Origin of the Physiology of the Brain

It seems that in any branch of science there is a decisive point which marks the beginning of its true development, i.e. a point at which the results of research cease to represent unrelated observations and begin to take the shape of an entity susceptible to interpretation, when students cease to be the "forerunners" (usually discovered *a posteriori*) and become regular architects of science in the field concerned. If this is agreed, then we must pick on the seventies of the past century as the turning point in the physiology of the brain. In those years, Hitzig and Fritsch demonstrated that electric stimulation of definite areas of a dog's cortex elicits movements of contralateral extremities, while destruction of the areas gives rise to temporary disturbances in corresponding motor functions. From that time onwards, in almost all countries, but especially in Germany and England, various fields of the cortex were intensively explored with the aid of two methods: stimulation of various points of the exposed cortex in an anaesthetized animal, and testing of the results of ablation of particular areas after the animal has awakened from anaesthesia. The investigations were so numerous and rich in results that by the turn of the century, the chart of the function of the cortex of animals (rabbits, cats, dogs, monkeys and apes) was essentially completed, and, what is more surprising, it has proved to be not very different from that worked out more recently with the aid of infinitely more perfect methods. The investigations demonstrated that the cortex comprises the so-called projective areas representing a cortical counterpart of particular receptor surfaces, the motor area, involved in voluntary movements of particular parts of the body, and areas of undefined function, which expand with the phylogenetic development of the brain and which were most frequently referred to as associative areas. As a rule, the results of the investigations were in conformity with the results of respective histological studies.

However, it is interesting to note that after this general scientific assault, when all the positions susceptible to conquest with the aid of the methods then available had been tackled, development along this line suddenly came to an end. It seemed that after the functional topography of the cerebral cortex had been mapped out, there was nothing more left to be done in the physiology of the brain.

The Foundations of Pavlov's Research

At that time, i.e. at the beginning of the twentieth century, there appeared, however, another essential trend in research on the functioning of the brain, a trend which was but slightly related to that previously referred to and started from different points of departure. The man who initiated it was Pavlov, who termed this field of science the physiology of higher nervous activity.

Pavlov's idea, which guided him throughout more than thirty years of work in this field, may be outlined thus:

1. The entire complex behaviour of the animal observed in its ordinary life is effectuated by the intermediary of the brain (especially of the cerebral cortex, as indicated earlier by Goltz's experiments with decorticated dogs). In other words, the brain represents the apparatus controlling this behaviour much in the same way as the spinal cord constitutes the apparatus controlling spinal reflexes. Consequently, just as by studying spinal reflexes we can learn about the functional mechanisms of the spinal cord, so understanding of the mechanism of the activity of the cerebral cortex may bring an analysis of the complex behaviour of the intact animal.

2. It follows that the behaviour of an animal is, like all other functions of the body, the subject of physiology. Psychological interpretations of animal behaviour are not only unnecessary but even misleading, since they cannot be tested experimentally and are speculative in character.

3. In undertaking the analysis of the complex behaviour of animals, we must first of all find out the elementary phenomena from which it is built up. Such an elementary phenomenon of behaviour is, according to Pavlov, a conditioned reflex, i.e. a reflex which has been acquired by the animal as a result of its individual experience. It is formed when an indifferent stimulus is followed by a stimulus eliciting an inborn (unconditioned) reflex, and consists in the indifferent stimulus acquiring the faculty of eliciting the same response as the inborn.

4. The "true" physiology of the brain is not so much concerned with the study of the effects of stimulation of the brain in anaesthetized animals—since such do not afford a picture of the normal functions of the organ—but rather with investigations involving conditioned reflexes in waking animals. The method of cortical ablation is by no means dropped, but its proper value will become apparent only when results of cerebral lesions are examined not with reference to superficial observation of the general behaviour of the animal, but with reference to their effect on definite conditioned reflexes.

Development of the Physiology of Higher Nervous Activity

Until the end of Pavlov's life the research work of his school followed almost exclusively the programme outlined above, and it can be divided (of course, rather schematically) into several stages.

Stage I. The first fifteen years were mainly devoted to studies on the fundamental properties of conditioned reflexes. In this stage, the foundations of our knowledge of conditioned reflexes were laid, foundations which have been changed but little to this day. First, the conditions of the formation of conditioned reflexes were studied in great detail. It was found that after a conditioned reflex to a certain stimulus has been formed, the same response is elicited also by similar stimuli (generalization). It was established that extraneous stimuli, applied simultaneously with conditioned stimuli, have an inhibitory effect on conditioned responses (external inhibition). It was shown that the disappearance of a conditioned reflex, which occurs when the conditioned stimulus ceases to "signal" the unconditional stimulus, involves the process of inhibition: i.e. that the conditioned reflex in such instances is not merely abolished, but is antagonized by a newly set up inhibitory reflex (internal inhibition). Various forms of this inhibition were subjected to detailed examination. Thus, the first stage closed with the establishment of the fact that alongside the excitatory conditioned reflexes there exist also inhibitory conditioned reflexes, which restrict and adjust the functioning of the former according to circumstances.

Stage II. During the next ten years studies on the dynamics of cortical processes predominated. While the preceding stage in the physiology of higher nervous activity was in character somewhat reminiscent of behaviourism, as it was chiefly devoted to discovering and systematizing the outward properties of conditioned reflexes, the main activity of the second stage was to determine the cortical processes underlying conditioned responses. Pavlov's physiological theory of these processes was based on the extensive and manifold experimentation of his followers on the mutual interrelations of excitatory and inhibitory conditioned reflexes when elicited in various combinations and temporal sequences. These experiments led Pavlov to the following conclusions concerning the dynamics of the cortical processes. He considered, first, that excitatory and inhibitory conditioned stimuli elicit the processes of excitation or inhibition, respectively, at the "point" of their impact in the cerebral cortex. Secondly, these processes, besides being conveyed to the further links of the conditioned-reflex arc, spread, or irradiate, over the given projective area, or even over the whole cortex; and then recede, or concentrate, back to the points of their departure. Thirdly, such expanding or shrinking foci of excitation and inhibition evoke on their periphery processes of opposite sign, which restrict their expansion (positive and negative induction). Thus, cortical function would represent a peculiar, continuously changing interplay of processes of excitation and inhibition arising every moment in various parts of the cortex, spreading and restricting each other according to the constantly changing stimuli from external environment.

It should be borne in mind that the picture of cortical dynamics, outlined here in a very abridged form, represents a certain theory (or rather a working hypothesis), deduced from experimental facts but by no means identical with them. Whether this theory is true or false depends on its congruity both with the whole body of experimental facts upon which it is based and with the general principles of nervous activity. However, owing to the strong faith placed in its correctness, the theory was accepted in Pavlov's school more and more as a dogma, and its statements were considered rather as experimentally proven facts, than as hypotheses necessitating further analysis.

Stage III. Finally, in the third stage of the research, Pavlov's attention was concentrated chiefly on phenomena of the functional pathology of cortical activity, and on closely related problems of typology. This vast field of investigation was opened up by the very important discovery that some combinations of excitatory and inhibitory conditioned stimuli may lead to nervous "conflicts" conducive to more or less persistent and pronounced disturbances in conditioned-reflex functions (so-called experimental neuroses). This provided a basis for an experimental pathology of the brain and for a detailed study of the aetiology, symptomatology and therapy of functional nervous disorders. The fact that the intensity and character of experimental neuroses depend largely on the individual characteristics of the animal prompted Pavlov to devote his attention to the typology, and led him to the establishment of his own classification of types of nervous system.

Pavlov's Theory and Contemporary Neurophysiology

Here an interesting problem confronts us. Why has the physiology of higher nervous activity failed to win general recognition as a new and important branch of neuro-physiology in spite of the fact that it is based on perfectly sound and rational premises? Why was it that during Pavlov's life-time research in this field was confined almost exclusively to his own laboratories, and that after his death the genuine Pavlovian line of research (not the applications of his theory to other fields) largely subsided, as if the subject had been exhausted and nothing was left to be done in this field? Why has the vast amount of work carried out by Pavlov's school in the course of some thirty years failed almost completely to elicit any response among physiologists? Is it because Pavlov's aim of physiological interpretation of the mechanisms of animal behaviour is in itself unattainable, or even fantastic, as some would like to think; or is it because neurophysiology is "not yet ripe" to tackle the problem, as others claim?

Some Soviet scientists and their imitators attempted to explain this state of affairs by way of ideological reasons, that is, by the reluctance of the West to acknowledge either the "materialistic" teachings of Pavlov or his authority. Nothing could be more misleading than such an explanation. Everyone who is even slightly familiar with world literature on this subject knows how great is Pavlov's authority among scientists to this day, to what extent the Western "war on Pavlovism" is but a myth, and how profoundly contemporary physiology of the brain is imbued with materialistic tendencies. Let us add that the development of American experimental psychology (behaviourism) was, and still is, greatly influenced by Pavlov's work, and that such terms as "conditioning", "reinforcement", and a host of others, have become its basic concepts. It may even be said that further experimental progress along Pavlov's line, though based on somewhat different principles and conducted by means of slightly modified methods, has been taken over by American psychologists, and their line of research is often referred to as "neo-Pavlovian".

In a monograph entitled "Conditioned Reflexes and Neuron Organization" I tried to make a thorough analysis of this situation, and arrived at the following conclusions. The failure of the physiology of higher nervous activity to become an integral part of contemporary neurophysiology is due to the fact that the model of Pavlov's theory of cerebral processes (developed chiefly in the second stage of his research work) was not congruent with the general model of nervous processes which was evolved from the evidence of numerous investigations concerning lower parts of the nervous system. This general model may be briefly described as follows. The entire nervous system of the higher animals, the brain included, is a vast net-work of neurons arranged in a definite order and representing the functional units of the system. Every neuron has a single long process or axon, dividing into numerous branches and extending either to executive organs or to other neurons with which it is connected by contact points, called synapses. Every neuron is a generator of nerve impulses, i.e. of electric disturbances carried along axons; reaching executive organs, they throw them into action, and reaching other neurons, they either excite them, i.e. cause them to generate new sets of impulses, or inhibit them, i.e. suppress the generating of impulses incited by other neurons. The system derives the necessary "energy" from receptors which, when excited by external stimuli, give rise to impulses conducted along afferent fibres to nerve centres. Thus, the nervous system represents a vast system of communication functioning on strictly defined principles.

Now, Pavlov's theory of cerebral processes was put forward independently of this general model (which was not yet then completely formed) and, as can easily be demonstrated, is at variance with it. The Pavlovian idea that cortical activity implies waves of excitation and inhibition spreading over the cerebral cortex and then concentrating at the original starting points, circumscribed by opposite processes on their periphery, cannot be harmonized with the model referred to above, and is unlike anything taking place in other parts of the nervous system. Consequently, Pavlov's theory, making use of terms borrowed from the language of neurophysiology, endows these with such a different meaning, or ascribes to them such specific qualities, that it becomes simply unintelligible to a neurophysiologist. The reason that animal psychology profited so much from the achievements of Pavlov's school is because this science discarded all the physiological concepts of Pavlov and limited itself to absorbing the merely empirical portion of his achievements.

In further sections of the monograph, I tried to demonstrate that it is possible to explain the wealth of factual material accumulated by Pavlov's school on the basis of modern neuron theory; and that the physiology of higher nervous activity, modified accordingly, can become a regular part of neurophysiology, offering possibilities of further development.

Behaviourism

At the turn of the twentieth century, independently of Pavlov's research work on conditioned reflexes, there developed in America another important line of investigations of animal behaviour, initiated by a prominent American psychologist, E. L. Thorndike, and generally known as behaviourism. The central idea of behaviourism was that all animal and human behaviour should be studied only empirically and that any reference to what the animal thinks or feels is superfluous.

It is beyond the scope of this paper to deal with this province of science in any detail; we are interested here only in those of its general features which are closely related to our own subject.

1. *The "model" of behaviouristic psychology*. Just as the basic concept in the physiology of higher nervous activity is that of the conditioned reflex, so the basic concept of behaviourism is "habit", i.e. any *acquired*, as opposed to *inborn*, motor activity of the organism. Most behaviourists are little concerned, if at all, with the physiological mechanisms of habits, their interests being primarily in the empirical properties of habit formation such as: the rate at which various habits are acquired and the dependence of that rate on all possible factors; the stimuli by which an animal is guided in dominating complex habits; the retention of habits, etc.

2. *Relation to physiology*. It is significant that Thorndike himself did not eschew the physiological approach to the phenomena he investigated and

some of his physiological conceptions, though now entirely forgotten, were highly ingenious. Some of the later authors took the same position, but others were more or less hostile to the physiological approach. The most prominent representative of the trend opposing physiology was the late Prof. C. L. Hull, the main founder of the formalistic system of animal behaviour. In Hull's system the connecting links between the stimulus and the reaction (in physiology, the nervous centres and their activity) are represented by so-called "symbolical constructs", such as: "strength of habit", "reaction potentials", "effective reaction potential", "drive", etc. The constructs are given no other meaning except that of a link between the factors acting upon an animal, and reactions observed.

However, in recent years, we are witnessing the tendency of behaviouristic psychology to come closer to the physiology of higher nervous activity. This fact is shown, for instance, by the dropping of the term "behaviourism" and substitution of the term "physiological psychology". This turn has been brought about mainly by the following factors:

(*a*) With the progress of methods applied in behaviouristic psychology it became apparent that, instead of the complicated mazes previously used, it is more promising to use simple methods, in which both the stimulus provoking a response, and the response itself are clearly manifest. This has brought together the concepts of habit and conditioned reflex, and has shown that the physiological approach to the phenomena under consideration is, after all, not so remote.

(*b*) In recent years there has been a renaissance in the study of the behavioural disorders following various cerebral ablations. It has become increasingly clear that, instead of observing superficially the general or "natural" behaviour of animals, it is much more fruitful to check the disorders by strict and definite behaviouristic tests. A pioneer of this line of research was Franz, at the beginning of this century, who was followed by Lashley, Kalisher and many others. So the co-operation between physiologists, and behaviouristic psychologists has become increasingly closer and has involved an exchange of ideas and the eradication of old prejudices.

(*c*) Finally, according to my own view, pure formalistic behaviourism is in the long run sterile. In fact, if we take the decision to refuse to accept psychological interpretations of animal behaviour, we are bound sooner or later to substitute physiological ones, otherwise we are doomed to remain on a purely empirical level without any possibility of creating a causal system of the facts observed. Therefore I consider that the gradual "physiologization" of behaviouristic psychology is an "historical necessity", and we are now witnessing the acceleration of this very process.

"Analytical" Physiology of the Brain

It is now time to return to the trend of development referred to at the beginning of our discussion, and to consider what we may call "analytical physiology", namely that which consists of studying the effects of direct stimulation on the exposed brain of anaesthetized animals. It is obvious that as long as electrical stimulation of various points of the cortex was almost the only method available, the scope of the investigations could only be very limited. In fact, it was exhausted when the topography of the motor areas of the cortex of various species of animals had been determined (Ferrier, Sherrington, and others) and when, by applying electrical stimuli varying in intensity, frequency and sequence, the excitability of this organ has been explored (Heidenheim, Graham Brown).

However, the situation has changed completely with the introduction of electronic amplifiers and sensitive oscillographs which make it possible to examine in detail the electrical activity of the cells of the brain. Forerunners in investigations of this kind, who used simply sensitive galvanometers, can be found as early as the nineteenth century, among them the eminent Polish physiologists Beck and Cybulski. However, genuine and systematic progress in the field began about 1930 with the work of Adrian, who succeeded in recording action potentials of the cortex of anaesthetized animals produced by stimulation of tactile receptors.

The principal idea of the method in question is very simple. "Natural" stimulaton of various receptors, or electrical stimulation of definite parts of the nervous system, generate nerve impulses which are conveyed along the nerve fibres and can be registered wherever the "electrical signals" from the site of stimulation reach. This affords a relatively easy means of learning what is connected with what in the nervous system, i.e. we may learn better than previously the functional structure of the system.

This method, usually referred to as neuronography, is applied on a vast scale in neurophysiology, especially in studies of the brain, and is now in use in almost all laboratories concerned. It has made it possible to learn about the interrelations between various parts of the nervous system in such intimate detail as was not to be thought of even a few years ago. The leap thus made in our knowledge of the functional structure of the brain is comparable to that produced in morphology by the advent of the microscope. A further step forward (which may be likened, in a way, to the application of the electron microscope) resulted from the use of microelectrodes and from the recording of action potentials from single nerve cells.

In what relation stand all these investigations, so vastly extending our knowledge of the structure of the nervous system, to the physiology of higher nervous activity? I would cite here a comparison I used elsewhere: "Imagine that our task is to discover what is going on in a certain huge and complicated secret factory without being provided with clues. On the one hand, we could do it by examining both the raw material supplied to the factory and the products delivered from it. If we were allowed to do this, we might change the raw material in order to see what changes there would be in the products, or even destroy some parts of the plant in order to see how that would affect production. From all this evidence we could form some idea how this factory works. Of course these conclusions would be only hypothetical, and must change according to our further knowledge of the factory. But, at the same time, in this way we could have a fair picture of what this factory was intended for. On the other hand, we could find a way into the factory and watch the machinery at work. This, one would imagine, would bring us nearer to a comprehension of functioning of the plant, but as there would be no guide to explain to us the logic and sequence of the processes of production it might happen that we should be at a loss—seeing all the details but unable to understand the whole." (*Brit. Med. J.*, 1949, *ii*, 944.)

While the divergence in the pathways of development of behaviourism and physiology of higher nervous activity was due rather to the different *approach* and tradition of the students engaged in the respective fields than to the difference of the fields under the exploration, the divergence between the physiology of higher nervous activity and the analytical physiology of the brain is, as can be seen from the above analogy, of quite another character. Here we are in fact unable to form a junction between the two lines of research, since we cannot understand what is the real functional significance of the interneural connections manifested in such detail by the neuronographical study. For example: what is the functional meaning of the supplementary projective areas in the cortex, of the various suppressing cortical areas, of the complicated connections between cerebral and cerebellar cortex found in such abundance in recent years? There is no possibility yet of giving any reasonable answers to these and many other questions, and all our guesses about them are both unfounded and incapable of being tested.

It seems to me that there are at present only a few ways of bridging the gap between these two lines of investigation. The best and most widely used consists in limited destruction of various areas of the brain or their connections, according to our neuronographic knowledge, and in studying the effect of this destruction upon various activities of the animal. With this method of investigation there is a good possibility of co-operation, as mentioned above, between neurophysiology and behaviouristic psychology. However, even more desirable in my view, would be a close liaison between the "analytical" approach, as represented by neuronography, and the "synthetic" approach, as represented by the physiology of higher nervous activity. For, although psychological tests can give us exact evidence of what is wrong in a particular sphere of behaviour after a particular cerebral lesion, they cannot supply us with the proper physiological explanation of the observed disorders. This can be done, by definition, only by the physiology of higher nervous activity. Therefore I am convinced that, without swift progress in this field, a progress which should supply us with a general framework, even though inexact and incomplete, of the normal activity of the cerebral cortex, our proper evaluation of the results of particular lesions and consequently our understanding of the functional significance of respective cerebral areas will be impossible.

Summary and Conclusions

From the foregoing analysis of the main trends in the development of the physiology of the brain and the connections and divergencies between these trends, one can discern, I think, the perspectives of further progress in this field.

To clarify the picture we might summarize the trends and indicate their mutual relations.

1. "Analytical" physiology of the brain, initiated by the Hitzig and Fritsch experiments concerning the electrical stimulation of the motor cortex, and recently expanded into a vast province of science through the methods of modern neuronography.

2. Physiology of higher nervous activity, founded and developed by Pavlov and his school, and concerned with the study of the central mechanisms governing acquired animal behaviour.

3. Behaviouristic psychology, initiated by Thorndike, the aim of which was to investigate acquired behaviour "as such", without reference either to psychological phenomena or to nervous processes.

When Pavlov, having laid the foundation of the physiology of higher nervous activity in the first ten years of research in this field, engaged in establishing a theory of cortical processes, the general laws of the functioning of the central nervous system were still largely unknown. Not finding a suitable basis for his research in the neurophysiology of that time, Pavlov went his own way, and created a quite independent system of ideas and hypotheses which, he believed, was adequate to explain the experimental facts rapidly accumulating in his laboratories. Thus a theory of cortical processes was established based on principles different from those which guided the research work concerned with other parts of the nervous system and carried out in other laboratories. It should be added that Pavlov frequently made it clear that he himself did not consider his theory as a dogma non-susceptible of further discussion. On the contrary, he saw its weak points and not infrequently modified it quite drastically. However, he failed to substitute for it a new compact system that would adequately account for the vast wealth of facts gathered by his school.

For these reasons, Pavlov's theory of cortical processes could not play the part of a framework in the physiology of the brain, as did Sherrington's concepts—developed at about the same time—as regards the functioning of the spinal cord; thus, the physiology of higher nervous activity failed to become "assimilated" by neurophysiology as an important new branch. This involved two important consequences. On the one hand, the behaviourists, though representing a trend quite close to that of the physiology of higher nervous activity by which they were greatly influenced, declined to assimilate Pavlov's theory of cortical processes (even in spite of their not infrequent good will), and turned away altogether from the physiological approach to the problems of behaviour, going the way of formalism. On the other hand, contemporary neurophysiology became mainly "analytical" in character, dealing primarily with the architecture of the connections between particular parts of the brain, and caring but little for their functional significance.

It is obvious that this abnormal situation could not continue indefinitely. Analytical physiology being increasingly successful, its students were bound to strive to understand the functional significance of the connections they detected. As a result they have been forced to call upon the assistance of either the behaviourist, or the physiologist of higher nervous activity. This has led to a lessening in the formalistic tendency of behaviouristic psychology, which manifests itself in the term "physiological psychology". Neuro-physiologists, on the other hand, realize with increasing clarity that effective help may be forthcoming chiefly from the physiology of higher nervous activity, for the latter operates with phenomena whose physiological mechanism is more or less intelligible.

Therefore it seems to me that we are now approaching a very important era in the development of the physiology of the brain: Pavlovian physiology of the higher nervous activity, behaviouristic or physiological psychology, and analytical neurophysiology of the brain, till now rather separate and even antagonistic, are beginning to merge and their respective students are beginning to understand each other. The study of the cerebral functions will no doubt continue to be the most difficult and the least accessible branch of physiology, but there are grounds for hoping that the factors obstructing its progress will eventually be removed.