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DEVELOPMENTAL PATHWAYS OF RESEARCH ON BRAIN-BEHAVIOR INTERRELATIONS IN ANIMALS

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It is quite natural that the celebration connected with an anniversary of a particular scientific institution induces us to look into the past and consider the development of the discipline which is represented by this institution. Of course, all reminiscences of this kind have a strong emotional character and this would certainly suffice for the speaker's undertaking the subject. I think, however, that besides the emotional aspect, such reminiscences are useful because the history of scientific ideas is undoubtedly important in properly evaluating the actual state of science, just as the developmental history of organisms is necessary for understanding their present state. I assert that these reminiscences are particularly important when they are based on the direct experience of the speaker and not on his second-hand knowledge based on a reading of old publications. Consequently, I consider the scientists of older generations to be particularly suitable for these reminiscences because the events which occurred in their disciplines 30 or 40 years ago are for them not bygone but reality, sometimes even more vivid than the present reality. Because I began work on the physiology of higher nervous activity exactly 40 years ago — my first paper with Stefan Miller was published in 1928 in *Comptes Rendus de Société de Biologie* — I would like to devote my present talk to the events which occurred during these 40 years.

However, before I turn to my proper subject, I would like to dwell

for a while on the earlier period which is as prehistoric for me as for you the early thirties: I would like to consider the situation at the turn of our century in the discipline to be discussed.

Now, when the problem of brain-behavior interrelations has become both interesting and fashionable, many people of the younger generation think that studies on this problem originated in the second half of our century. This is, however, very far from the truth. In fact, first studies in the field of the modern physiology of the brain, initiated by the pioneer work of Flourens, Hitzig and Fritsch, Golz, Ferrier and others, consisted in ablations of various areas of the cerebral cortex in animals and in observations of how the animals behaved after these operations. In this way, attempts were made to learn the functional significance of a given cortical area. Thus, in the very beginning of research on brain activity, this organ was *a priori* regarded as a system serving to control animal behavior. The task of the investigators was to understand in which way this control is executed. These investigations became a foundation of our knowledge on brain activity, a foundation on which all later research was to be based.

It should be stressed at once that the chief drawback of these investigations was that at that time the specialized experimental methods in the field of animal behavior and learning, such as mazes, discrimination boxes, and above all, the methods based on conditioning, were very poorly developed and failed to penetrate into physiological circles. Therefore, these scientists were fully satisfied with the *general* observation of brain lesioned animals and with their neurological examination. Only a few authors, among them the Russian physiologists Pavlov and Bechterev (and their collaborators), the German psychologist Kalischer and the American psychologist Franz, began to apply behavioral tests to the study of animals with brain lesions.

After this short "prehistoric" introduction with regard to my own past we can turn immediately to the early thirties, that is to the period when I began to work on the problems of the brain-behavior interrelation. At that time experimental work on the acquired behavior of animals was developing at full speed, that is, work on conditioned reflexes in Pavlov's terminology, or habits, according to American students. Therefore, an urgent need emerged to create a theoretical basis, or to be more exact, a framework, in which the rapidly accumulated experimental data might be organized. And just at this point there arose acute controversies whose traces we can still observe or even feel at present. Also at that time extensive studies were published which depicted and synthesized the achievements and theoretical attitudes of particular scientists and their co-workers. These studies have played a most important role in the fur-

ther development of the discipline with which we are concerned. In particular I have in mind the following works:

1. *Conditioned reflexes, an investigation of the physiological activity of the cerebral cortex*, by I. P. Pavlov, a book which appeared in 1927 and was immediately translated into English, French and German.

2. *Individually acquired activity of the central nervous system*, I. S. Beritov's book which was published in 1932.

3. *Brain mechanisms and intelligence*, a monograph by K. S. Lashley, published in 1929.

4. *Purposive behavior in animals and man*, a book by E. C. Tolman, published in 1932.

5. *Principles of behavior*, by C. L. Hull, a book which appeared only in 1943, though the views of the author were known earlier from his previous publications.

6. *The behavior of organisms*, by B. F. Skinner, published in 1938.

I will begin my survey of the scientific attitudes concerning animal behavior with Pavlov. It is worth mentioning here for those who may not realize it that when Pavlov was starting, at the beginning of our century, his research on the physiology of the brain, he was already a world renowned scientist who had laid the foundations for the modern physiology of the digestive glands, work for which he won the Nobel Prize in 1904. While studying the secretion of salivary glands in dogs Pavlov came upon the phenomenon of the so-called psychic secretion which occurs in humans as well as in dogs; it consists in the occurrence of salivation not only when food is in the mouth but also when a subject sees the food, sniffs it and so on. Pavlov regarded psychic salivation as a physiological phenomenon, basically the same as purely reflex salivation; therefore, he referred to it as a conditioned reflex. According to Pavlov, the only difference between the conditioned reflex and the inborn or unconditioned reflex was that the conditioned reflex is more complex, that it is acquired according to an animal's experiences and that it depends on the higher centers of the nervous system. Pavlov clearly understood that the salivary conditioned reflex may be regarded as a convenient *model* for the acquired activity of the animal, of the activity controlled by the brain and particularly by the cerebral cortex. Just as on the basis of the course of spinal reflexes we may draw conclusions about the properties of spinal centers, so on the basis of salivary conditioned reflexes we may learn about the properties of the cerebral centers. To put it in modern language, one can say that from knowing the input signals of a given complicated steering design — in this case conditioned stimuli — and its output signals — in this case salivation — we can make conclusions concerning the internal structure of this design. In this way,

the tremendous research work of Pavlov and his many co-workers initiated the field which he called the physiology of higher nervous activity. It is highly significant that till the end of his life Pavlov remained faithful to the salivary glandular reflex as the indicator of the nervous processes he investigated. For, on the one hand, this approach made an excellent *quantitative* method of animal responses and on the other hand, he was thus able to avoid the immense complication and variety of phenomena involved in the motor behavior of animals. Pavlov was fully aware that the laws governing salivary conditioned reflexes apply to all other conditioned reflexes connected with other activities of the organism, a fact which was confirmed in further studies.

It is worthwhile to draw your attention to the interesting circumstance that Pavlov, in the first decade of his work on conditioned reflexes, continued to follow the old tradition of using the ablation method to study the brain. Thus, after the formation of certain conditioned reflexes in dogs, some parts of the cerebral cortex were removed and the disorders in these reflexes were examined. From this procedure, conclusions might be reached as to the functional significance of a given cortical area. However, in the following years Pavlov totally abandoned this line of research and devoted himself completely to the study of conditioned reflexes in dogs in which the only surgery done was providing the fistula of the duct of one of the salivary glands in order to measure conditioned and unconditioned salivation. This change of the line of research occurred because the study of conditioned reflexes established to various stimuli and their manifold combinations provided so much information about brain activity that the methods of cerebral lesions seemed to Pavlov superfluous. In other words, Pavlov adhered to a wise principle, formulated by Von Holst forty years later to the effect that brain research at its present stage of development should be concerned with the questions of "how" and "why" rather than with the question "where". And Pavlov tried to answer the questions of "how" and "why" precisely by changing and combining the signals entering the steering system and recording the only output signal he utilized, namely salivary secretion.

In Russia, or rather in Georgia, in the second decade of our century there arose another scientific center whose work to a great extent followed the line of Pavlov's research. This center was created by I. S. Beritov. His experimental method was basically the same as that of Pavlov, except that his indicator of cortical activity was not the alimentary conditioned reflex manifested by salivation, but the defensive conditioned reflex manifested by leg flexion to a conditioned stimulus signalling the stimulation of the paw by electric shock. From the very beginning of

his work in the field of conditioned reflexes (which he called "individual reflexes" in contradistinction to "species reflexes") Beritov was a vehement opponent of Pavlov.

Although Beritov did not question the experimental data obtained in Pavlov's laboratories, he denied the soundness of Pavlov's conclusions concerning the mechanism of the steering system, a mechanism which was the purpose of both these scientists' search.

It is not difficult to find the genesis of this controversy. Whereas Pavlov came to his study of the physiology of the brain from a very remote field of research — the physiology of digestion, Beritov was always a pure neurophysiologist and he tended to reconcile the principles of brain activity with those established for lower levels of the nervous system.

Since I am taking the role of a chronicler in these reminiscences I do not intend to enter into the details of this dispute or to evaluate who was right and who was wrong. I wish only to note that, as it follows from my previous considerations, the argument between the two scientists, or rather Beritov's attacks on Pavlov's theory, had a purely matter of fact character, since the principal attitude of both was identical: both attempted to discover the principles of brain activity on the basis of its input and output.

Now I will turn to a discussion of another opponent of Pavlov whose standpoint was much more at variance with him, and whose views influenced to a great extent the formation of scientific attitudes of the students of the discipline. I have in mind the American scientist K. S. Lashley, the author of a great number of experimental papers and the famous book *Brain mechanisms and intelligence*.

For the better information of the audience I would briefly like to present one of the most important series of experiments conducted by Lashley and conclusions he drew from them.

Lashley performed experiments on rats and trained them to run mazes of various complexities. He compared the rate of learning in normal rats with those having cerebral lesions of different sizes and locations. The results of these experiments were rather unexpected. First, it was found that the larger the part of the cerebral cortex removed, the slower the animal's mastering of the maze habit. Secondly, it was found that impairment of learning did not depend on the localization of the sustained lesion. From these experiments Lashley drew the following two conclusions: first, that the amount of the remaining cortical tissue determines the learning ability — a principle which Lashley called the law of mass action; and second, that various parts of the brain are in

this respect equivalent — a principle he called the equipotentiality of the brain.

I do not intend to describe other experiments of Lashley here, among others those which partially weakened the above thesis; my purpose is to emphasize the principal idea of his research, an idea which he held till the end of his life. This idea may be formulated as follows: no place in the brain exists where memory traces, or engrams, are maintained because as a matter of fact they are everywhere and nowhere; in consequence, any connectionistic conception of learning and conditioning is *a priori* doomed to failure. Hence Lashley denied the concept of the conditioned reflex as an elementary phenomenon of brain activity, based on a connection between the center of the conditioned stimulus and the center of the unconditioned stimulus.

It is most interesting to compare the scientific attitudes of Pavlov and Lashley. With regard to their *experimental* methods, Pavlov worked on dogs studying their salivary conditioned reflexes; Lashley worked mainly on rats by means of the maze method and the discrimination box of his invention. However, the more important difference is that whereas Pavlov as we have seen quickly abandoned cerebral surgery, insisting on answering the questions of "how" and "why", Lashley was concerned for his whole life with the problem of "where" and tended to answer this question by studying the effects of lesions of various parts of the cerebral cortex on the performance of specific tasks. Finally, whereas Pavlov was, in a manner of speaking, a "positivist" in science, that is he tried in every way possible to *understand* the phenomena he investigated by putting forward one hypothesis after another without fear of mistakes, Lashley was a typical "spirit of negation" and his chief purpose was to show: "you are wrong, your explanations are false". He was *sui generis* a devil's advocate in science, and not at all in the pejorative sense of the term.

Though I am not in the least abandoning my role of a chronicler I must state that Lashley's criticism of Pavlov's theory was not quite just and was based to a large extent on misunderstanding. For Pavlov was not only a great scientist but a very wise man as well, and he perfectly realized the immense complexity of the problem of brain activity. Furthermore, results were obtained in his laboratories which were similar to those discovered by Lashley — after the ablation of the visual area of the cerebral cortex differentiation of light intensity was unimpaired, and after ablation of the auditory area the differentiation of tones was preserved. Pavlov himself created the concept of "mechanical immunity" of cerebral tissue, a principle now called the infallibility of steering systems. On the other hand, Lashley fell into cognitive nihilism

too soon, he gave up too quickly as far as a positive explanation of his facts was concerned; for instance, he did not consider the possibility of the existence of *parallel* nervous pathways on different levels of the nervous axis, pathways which could replace each other in case of destruction of one of them.

In spite of all these reservations and discussions resulting from the immense complexity and, I would say, mystery of the steering system which is the brain of higher animals, Lashley held to the physiological standpoint consistently; he only insisted on that we cannot explain through connectionistic concepts where memory traces are laid down, and he maintained that the principles of brain activity are rather different from those which we usually imagine.

However, the scientific attitude of the group of scientists to whom I now turn is quite different. I have in mind Hull, Tolman and Skinner. And here again I must give a short "prehistoric" introduction.

The American psychologist Thorndike is generally considered the father of American (and even world) animal psychology based on experimental methods. The scientific attitude of Thorndike was very near to that of Pavlov — he claimed that the study of animal behavior should be purely objective and should not resort to introspective explanations. And Thorndike did not avoid attempting physiological explanations of the facts he obtained. Then, in the second decade of our century Watson, the famous American psychologist appeared on the scene; he regarded the objective approach to the study of both animal and human behavior as his main methodological program, and he has advanced a new scientific doctrine called by him "behaviorism", a doctrine which played an enormous role in the further development of behavioral sciences. It should be noted that at that time the news of Pavlov's early investigations of conditioned reflexes reached America and Watson accepted them enthusiastically, recognizing Pavlov as a chief prophet of behaviorism. Thus, in the thirties, the period in which we are interested here, behaviorism was already a widespread and generally acknowledged scientific doctrine.

And now something quite unexpected happened which is somewhat difficult to explain. Students appeared who, holding the objectivistic position in behaviorism and dismissing the subjectivistic treatment of animal behavior as unscientific, fought with equal energy against the *physiological* treatment of behavior. As a result there arose a large scientific discipline which deprecated both subjectivistic psychology and physiological approach to the study of behavior.

This historical event which we witnessed is all the more strange since the tendency to physiologize arose rather early in psychology, even before Pavlov, and was widespread at the end of the nineteenth and

beginning of the twentieth century. We should remember that the German psychologist Wundt, at the end of the nineteenth century, proposed the term "physiological psychology" he used as the title of his three volume treatise which played such an important role in psychology's development. In other words, the alliance between brain physiology and psychology was something rather natural and its strengthening was to be expected with the development of the physiology of the brain. Therefore, the break in this alliance committed by behaviorists in the thirties was quite unexpected.

Since I am not a behaviorist and I was not a direct witness to this break I cannot offer reasons for it. The eminent Canadian psychologist D. O. Hebb, who belongs to the physiologizing group of psychologists, asserts that the blame for this process should be placed precisely on Lashley whose nihilistic attitude toward all theories of physiological explanations of animal behavior and whose continuous propagation of the position of "ignoramus" was responsible for the credibility gap in physiology as a discipline from which psychologists could expect assistance.

Let us see what offer was made by behaviorists in exchange for the subjectivistic attitude they abandoned and the physiological attitude they rejected. Here two lines of thought may be discerned. One line of thought is represented by Hull, Tolman and many of their followers. These scientists professed various *formalistic systems*, involving "intervening variables" put between stimuli and reactions, and accounting for their interrelations. The difference between this approach and that of a physiologist is quite essential. If a physiologist puts forward hypotheses concerning the mechanisms of the brain, he *must* take into account, and make use of the *general principles* of the functioning of the nervous system. On the other hand, for a behaviorist such limitations do not exist, since his "constructs" linking the stimuli with the reactions are purely formalistic and devoid of any actual content.

What was the attitude of Hull and his followers to the achievements of Pavlov's school? It was most positive as far as their behavioral aspects were concerned. Hull utilized the experimental results of the Pavlovian school to a great extent and he included these results into his formalistic system. Accordingly Hull's doctrine is often referred to as the neo-Pavlovian doctrine.

Here for example is a curiosity of Hull's thinking. In his system the quantitative relations between the stimulus and the response play an important role and, following Pavlov, he introduces intervening variables representing both excitation and inhibition. Hull proposes the *units* of these variables and denotes the unit of excitation as "Wat" from the

name Watson and the unit of inhibition as "Pav" from the name Pavlov. Consequently a given response may be the result of so many Wats minus so many Pavvs.

I will now turn to considering another principal personality in behaviorism, in whose hands this doctrine became even more radical or positivistic than with Hull, that is to Skinner. Skinner created an experimental method consisting in that the animal performs a definite simple movement — a rat presses a small lever and a pigeon pecks a small window — under alimentary motivation. Thus, in principle this method is the same as the method of Type II conditioning introduced by Miller and me. However, the utilization of this method in Skinner's experiments is quite different. Skinner introduced various "schedules of reinforcement": in fact one can reward the animal for every lever press (or peck), or for each definite number of presses, or one can reward only those presses which follow one another with a given frequency, and so on; since the schedules of reinforcement are programmed beforehand and fully automatized, the animal is left to itself for hours and even days.

Now Skinner is neither interested in the physiological mechanisms controlling the animal's activity nor even, so to speak, in imaginary mechanisms provided by Hull and others. He is interested only in the purely empirical level of the phenomena concerned and does not go beyond this level. In spite of the fact that such an approach may seem to many people completely sterile, it won a great many followers, and the "Skinner box" is one of the most popular behavioristic methods. For Skinner the ideal theoretical model of his approach was Newtonian mechanics, and Newton's famous statement "hypoteses non fingo" was the leading idea of scientific conduct for Skinner. This being so, there is no wonder that Skinnerians form a sort of isolated group, or rather sect, possessing their own journal with the significant title: *The Journal of Experimental Analysis of Behavior*. The group has its own very sophisticated problems in trying to discover which refined schedules the animal is able to master.

The above somewhat pejorative description of Skinnerism is not quite fair because some investigations based on the Skinnerian method can be utilized in problems going far beyond the field of pure empiricism and have great significance in the field of brain physiology and brain pharmacology. Consequently one may note an interesting difference between the *intentions* of a scientist when he invents a new method and an *ultimate use* of that method. The method of conditioned reflexes was invented by Pavlov for the study of brain activity, but it has played a tremendous role in behavioristic psychology which repudiates the physiological approach to the phenomena in question. In contrast, the Skinner method, which was invented for the creation of a purely positivistic

and empirical system of behavioral science, is a valuable instrument for the study of brain-behavior interrelations.

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Such were the discussions and controversies in the fourth decade of our century, just before the terrible and tragic cataclysm of the Second World War. However, as is seen from the history which we experienced ourselves, even the most terrible cataclysms can only *disturb* the progress of science, just as logs thrown into a river can disturb its course, but cannot *inhibit* it. Therefore, after the War the course of investigations continued and the old discussions and controversies have revived. Because of the rapidly running time of this lecture I am not able to trace the further development of the scientific events which were described here, and so I shall jump directly to the year 1968 to see how those *dramatis personae* whose ideas I presented above look like now.

Let us begin again with Pavlov. Pavlov died in 1936. There was a time when the significance of his achievements seemed to decrease, but soon there was a new turn of events. For, with the improvement of methods of brain physiology, and particularly, as experimental neurosurgery reached a high technical level, when it became possible to perform precise operations on the brain taking into account its anatomical organization, when it became possible to implant electrodes into definite places in the brain and stimulate these places in waking animals, and, finally, when it became possible to record action potentials from neuronal groups or even single neurons in these animals, then at last, thirty years after Pavlov's death, his dreams were fulfilled. The physiology of the brain as a system steering animal behavior received a strong developmental impulse because it became possible to look into this system and directly observe its activity. And then the method of conditioned reflexes — those simplest and best understood responses controlled by the brain — immensely gained in significance. Therefore, in more and more laboratories devoted to the study of brain physiology, the conditioned reflex methods in their various forms found their proper place.

Concerning the main opponent of Pavlov, I. S. Beritov, he continues with great vigor to pursue the line of investigation he began about 50 years ago, broadening the scope of research and deepening his physiological concepts on the mechanisms of the brain function.

In connection with an enormous development of the physiology of higher nervous activity, or physiological psychology, or neuropsychology, or physiology of the integrative activity of the brain — this last term seems most suitable to me — this scientific discipline overtakes the positions previously occupied by behaviorism. For, one cannot continue to

treat the animal's skull as a black box about whose interior one can know nothing, at a time when one is able to look into this interior by means of electrodes recording action potentials, to remove bits of this interior by neurosurgical operations, or to influence directly this interior by electric stimulation or psychotropic drugs.

If we depict the present state of behavioral sciences in the general terms, its most accurate characteristic seems to be the following: All the investigations connected with the direct manipulation of the animal's brain, including the vast repertory of behavioristic methods, were assimilated by physiology. On the other hand, investigations concerning various forms of acquired animal behavior carried out by the pure input-output methods without intruding into the brain itself are now polarized: either they preserve the character of formalistic behaviorism, or they approach physiology more and more.

To end, a few words about Lashley. Lashley died in 1958. The edge of his nihilistic theoretical attitude discussed earlier seems to have become less sharp, simply because as we better and better understand the principles of the activity of great nerve nets, the problems which seemed unsolvable in Lashley's time do not look so hopeless now. And although we are still very far from their solution, we at least see the beginning of paths which we can enter. Furthermore, it should be remembered that Lashley was one of the main pioneers of the application of ablation methods to behavioral sciences, and his research work in the field of visual perception in rats, the work which showed that, after all, the cerebral cortex is not so anonymous and equipotential as he propagated, has played a very important role in physiological psychology.

It can be seen from this epilogue that at the end of his narration the chronicler suffered a breakdown in his objectivism and gave opinions about the values of our distinguished precursors, opinions with which one can agree or not.

But this is the fate of the majority of chroniclers and perhaps it is not so bad. For if a narration about the past can serve to pave the way for future research, we cannot avoid giving such opinions, because our decisions about the further development of our scientific discipline depends on how we evaluate various aspects of the past. The only important thing is to clearly separate the field of facts from the field of their evaluation; for, the history which I have just presented shows how much these evaluations can change in the course of years, while the factual data, if they are correct, remain the same.