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JERZY KONORSKI'S THEORY OF CONDITIONED REFLEXES

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The 1st of December 1983 marked the eightieth anniversary of the birth of Jerzy Konorski, who founded the Polish school in neurophysiology. He was the author of more than 180 scientific publications, written and printed in various languages: Polish, French, German, Russian and English. For many years his writings stimulated students of animal and human behavior, admired by some and attacked by others.

STAGES OF THE DEVELOPMENT OF KONORSKI'S CONCEPTUALIZATION

Owing to his knowledge and inquisitiveness, his energy and industry, Jerzy Konorski exerted a vital influence on the development of the physiological sciences and experimental psychology, in Poland as well as elsewhere. His most important achievements are concerned with three problem areas. First, Konorski and his friend Stefan Miller, while students, distinguished instrumental conditioned reflexes as a separate type of acquired behavior (20). In a series of pioneer studies they demonstrated basic differences between instrumental conditioned reflexes and those classically conditioned reflexes, initially described and studied by Pavlov (14, 15). Second, he reinterpreted the results of research on conditioned reflexes on the basis of the mechanisms of Sherringtonian neurophysiology which focused on the functioning of lower levels of the nervous system. Owing to his work "Conditioned reflexes and neuron organization" (10) published in 1948 in England, Konorski became one of the founders of the contemporary neurophysiology of the brain. Third, he created a general model explaining perceptual processes. Ba-

sed on that model, in a book on "Integrative activity of the brain" published in the United States in 1967 (11) and translated into Polish in 1969 (12), he analised brain activity as a complex cybernetic system which directs the functioning of the organism as a whole.

Soon after Konorski's death, there appeared publications describing him as a scientist and a man, analysing his scientific output and its importance for brain research (22, 28, 29, 34). Two international symposia were dedicated to him and to the problems on which he had worked (5, 35), and at many other conferences and congresses special sessions were dedicated to his research efforts. Discussions held at that time led to the conclusion that in the general opinion of scholars, the theory of instrumental conditioning is Konorski's most important contribution to brain research.

During his 45 years of scientific work, Konorski several times modified his opinions on the mechanisms responsible for the acquisition and performance of instrumental responses. However, the analysis of experimental data that produced these modifications exceeds the scope of this paper. I shall therefore confine myself to demonstrating the effect of the instrumental response theory on the change in the substance of one of the fundamental concepts in neurophysiology — the conception of the reflex.

THE EVOLUTION OF THE REFLEX CONCEPT

If we analyze the evolution of the reflex concept over the last 150 years, we shall be able to perceive a definite trend. At first, reflexes were defined as relatively simple reactions performed almost automatically when a specific stimulus was perceived by the nervous system. Later, owing to discoveries of such scientists as Setchenov, Goltz, Sherrington, Magnus and others, the scope of this term was gradually enlarged. These scientists showed that simple reflexes with centers located at the lower levels of the nervous system are subject to changes under excitation induced in other parts of the nervous system. These discoveries changed the original view on the invariability of reflexes. Although the interactions investigated among various centers took place through inborn nervous connections, these new data prepared the ground for the application of the reflex conceptualization to the study of behavior acquired in the ontogenetic development of animals and humans.

This turning point was reached at the beginning of the 20th century by Ivan P. Pavlov. The basic information was that salivation occurs not only in response to the stimulation of taste receptors, but also in response to other stimuli regularly accompanying food presentation. Thus, stimulation of the center responsible for salivation occurs not only through

the genetically coded nervous pathway from the taste receptor, but also through pathways from other receptors: somesthetic, visual, auditory, which in untrained animals do not cause excitation in the center controlling the functions of the salivary gland. Based on that observation, Pavlov introduced two new terms (23). The genetically coded reaction of the salivary gland caused by food presentation was named the "unconditioned reflex", whereas the reactions of that organ caused by other stimuli regularly preceding food presentation were called the "conditioned reflexes" resulting from the process of learning. Similarly, unconditioned and conditioned stimuli were distinguished. To turn a neutral (e.g., a definite sound) into a conditioned stimulus, only its regular association in time with the unconditioned stimulus presentation was required. When the sound ceased to be reinforced by food presentation, the conditioned response disappeared, the conditioned reflex became extinguished. The conditioned reflexes described by Pavlov have been accepted as a universal method of studying the plasticity of the highest level of the nervous system — the cortex.

THE DISCOVERY OF INSTRUMENTAL REFLEXES

At the time when Pavlov's popularity reached its summit, two totally obscure students of the faculty of medicine at the University of Warsaw discovered a certain gap in his reasoning. They arrived at the conclusion that Pavlov's model of conditioned reflex was not sufficient to explain the acquired motor behavior of animals and men. The association in time of conditioned and unconditioned stimuli does not ensure the learning of a definite motor conditioned response. A logical analysis of the conditions necessary for the elaboration of motor conditioned reflexes led to the discovery of four experimental procedures known today as reward training (Fig. 1*C*), omission training (Fig. 1*D*), avoidance response training (Fig. 1*E*) and punishment training (Fig. 1*F*). In one of their first papers, published in 1928, Konorski and Miller presented the results of experiments on dogs which proved the effectiveness of these four methods of training motor conditioned reactions (20).

Thus, 25 years after Pavlov's discovery of conditioned reflexes, now called classical, another type of conditioned reflex, now called instrumental, was discovered in Warsaw. In their writtings Konorski and Miller named them "Type II Conditioned Reflexes", as distinguished from Type I Conditioned Reflexes discovered by Pavlov.

The discovery of instrumental conditioned reflexes considerably enlarged the conceptualization of the reflex. That the authors were conscious of this expansion was confirmed by the last words of the mono-

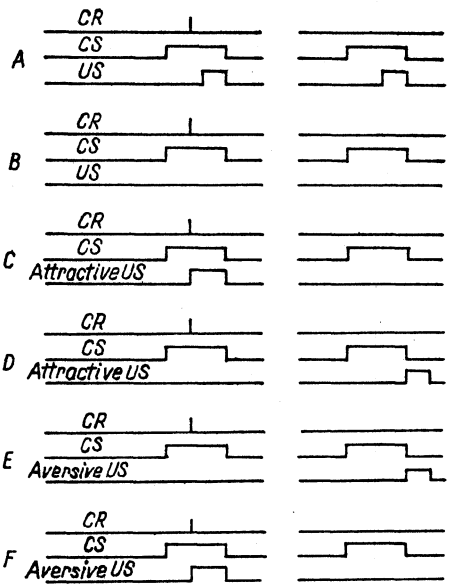

Fig. 1. Relations between the conditioned stimulus (CS), the conditioned response (CR) and the unconditioned stimulus (US) in a variety of classical and instrumental conditioned reflexes. On the left are presented relations between CS and US if the CR is performed, on the right are the relations between CS and US if the CR is not performed. The time course is from left to right in each graph. *A*, classical excitatory conditioned reflex. *B*, classical inhibitory conditioned reflex. *C*, reward training. *D*, omission training. *E*, avoidance response training. *F*, punishment training.

graph by Konorski and Miller, summing up the results of their first period of investigations: "By introducing type II conditioned reflex to the physiology of the cortex we include in the scope of physiological research a vast area of the organisms' motor behavior, hitherto accessible to psychology only" (14, p. 161).

The discovery of instrumental reflexes began a long lasting process of reevaluation of conditioned reflex theory, a process which is still far from concluded. Thousands of scientists working in hundreds of laboratories participate in this process. To Konorski's greatness is testified the fact that discoveries essential to the process were made by himself or by his students, and that many important hypotheses were formulated in his writings.

A direct effect of the discovery of instrumental reflexes was the change in the substance of two fundamental conceptualizations introduced by Pavlov: the conditioned stimulus and the unconditioned stimulus. Linking the conditioned with the unconditioned stimulus leads

to their association. As the result of association, the conditioned stimulus becomes, according to Pavlov, a "substitute" for the unconditioned stimulus and evokes a response similar to that observed to the unconditioned stimulus presented alone (24). In contrast to that in instrumental conditioning the conditioned response differs as a rule from the response evoked by an unconditioned stimulus. The conditioned stimulus rather signals the possibility of getting food, or of avoiding a painfull stimulus. Food, or other appetitive unconditioned stimulus, in instrumental conditioning plays the primary role of reward for the execution of a definite motor act, and food omission is a punishment for an incorrect instrumental response. While classical conditioned responses get reinforced only by the pairing of the conditioned and unconditioned stimulus, the reinforcement of instrumental responses takes place according to a more complex rule, both with and without the use of the unconditioned stimulus. Analogous relations appear with the use of pain or of other aversive unconditioned stimuli.

With regard to the different role of unconditioned stimuli, it became necessary to introduce the concept of drive (motivation) to the theory of conditioned reflexes. According to Pavlov, the level of hunger affected only the magnitude of conditioned response, whereas to evoke an instrumental appetitive response, a definite level of drive center excitation is a required condition. In the first period of training, the hunger drive motivates the animal to perform various motor acts, one of which — the correct one — subsequently gets fixed by food presentation, while other, incorrect responses not leading to food presentation become extinguished. For that reason instrumental reflexes were often called drive reflexes.

In Pavlov's original conceptualization the anatomo-physiological substrate of conditioned reflexes was the formation of connection between the cortical representation of the conditioned stimulus and the cortical representation of the unconditioned stimulus. According to Konorski, the simplest diagram of the instrumental reflex arc must also enclose the drive center. Since the anatomo-physiological substrate of drives are, in the first place, subcortical structures, these structures should, beside the cortex, be also included in the process of acquisition and performance of conditioned responses. The rapid development of research on the limbic system over the last decades is connected, to a great extent, with the discovery of instrumental reflexes and the use of instrumental response methods in the study of drive and emotion problems. The conditioned reflex theory, called in Pavlov's lifetime the theory of cortical processes, became a theory of functioning of the whole brain.

That change in the anatomo-physiological substrate of conditioned

reflex was bound to have farreaching consequences. It was necessary to accept physiological mechanisms common for the cortex and subcortical structures, responsible for acquisition, performance and extinction of conditioned responses. This task was undertaken by Konorski. The conditioning process was presented as a phenomenon based on the integration of nerve cells by means of synapses. Mechanisms thoroughly investigated in the spinal cord were consistently applied to brain functions. Many conceptualizations formerly used in Pavlov's "theory of cortical processes", such as irradiation and concentration of excitatory and inhibitory processes, positive and negative induction, etc., were suddenly discarded or radically and substantially changed.

Konorski's fundamental reinterpretation of the conditioned reflex theory, presented in his monograph "Conditioned reflexes and neuron organization" (10), was met with a total incomprehension by American behaviorists, incapable of accepting his neurophysiological theory, with a lack of interest by many neurophysiologists, and with an attack from scientists remaining under the strong influence of Pavlov. In the early 1950's Konorski's ideas became an object of severe criticism. The analysis of the merits and the extra-scientific motivations underlying some of this criticism make interesting material for the historians of science. Fortunately, the director of the Institute of Experimental Biology was, at the time, Professor Jan Dembowski, a great scholar who understood the logic of scientific development and did not easily yield to moods prevailing in the so-called scientific circles, nor to pressure from some administrators of science, sensitive to these changeable moods.

THE RELATIVITY OF DIVISION INTO EXCITATORY AND INHIBITORY CONDITIONED REFLEXES

Behavioral experiments resulting from the new theoretical approach led to a change of opinion on the problem of internal inhibition, crucial for the conditioned reflex theory (30). In conformity with Pavlov's experiments, the conditioned reflex becomes extinguished when the conditioned stimulus ceases to be paired with the unconditioned stimulus. It was believed that during such training an inhibitory process develops in the conditioned stimulus center and supplants the previously developed excitatory process. The very name of the procedure used in these experiments — extinction — testifies that Pavlov considered the inhibitory training as secondary to the training of excitatory conditioned reflexes. Konorski, on the other hand, proved that conditioned stimuli unassociated with unconditioned stimuli and used in experimental sessions among excitatory conditioned stimuli of a different modality, ac-

quires strong inhibitory properties (16, 17, 25, 26). Such conditioned stimuli have been called "primary inhibitors". These data showed that besides the excitatory classical conditioned responses (Fig. 1*A*) there should also be distinguished, as a separate variety, the inhibitory classical conditioned responses (Fig. 1*B*). The Pavlovian extinction procedure, according to Konorski, consists in the elaboration, alongside the already existing interneuronal connections responsible for the execution of excitatory conditioned reflex, of new connections responsible for the inhibitory conditioned reflex. In effect, with the application of an extinguished conditioned stimulus, connections responsible for the performance of both inhibitory and excitatory conditioned reflexes start to operate. This dual nature of the "extinguished" conditioned stimulus can be easily demonstrated by tests (18). The homogeneous nature of the "primary inhibitor" was proved experimentally later, after the training method called "differentiation without errors" had become widespread (1, 27).

The experimental procedure where in sucessive trials use various conditioned stimuli, some paired and some unpaired with the unconditioned stimulus, is now called "Pavlovian differentiation procedure". In Pavlov's experiments the differentiation of stimuli resolved itself into elaborating classical conditioned responses, excitatory to some stimuli, inhibitory to others. Introducing instrumental reflexes to the arsenal of conditioning experiments greatly increased research possibilities. New differentiation procedures and new terms appeared. Now it is believed that the essential thing in differentiation procedure is the elaboration of different varieties of conditioned responses to respective conditioned stimuli used in the experiments.

If to one stimulus an alimentary instrumental response is elaborated by reward training, and to another stimulus — an inhibitory classical conditioned response, such a procedure is called "asymmetrical differentiation". If, however, with the same alimentary response to one stimulus, an instrumental response to the other stimulus is trained by omission training, the procedure is called "symmetrical differentiation" (8, 9). Konorski and Miller used a differentiation procedure in which a classical inhibitory alimentary response was elaborated to one stimulus, and with the other stimulus omission training was applied (15). The mere confrontation of these three differentiation procedures shows the relativity of division into inhibitory and excitatory conditioned reflexes. In one instance, an instrumental response trained by omission training my have the nature of an inhibitory reflex (in symmetrical differentiation), in another instance of an excitatory reflex (in the cited experiment of Konorski and Miller).

In his last monograph Konorski offered an opinion that inhibitory conditioned responses are the result of the mutual interaction between two arcs of excitatory conditioned reflexes. In the case of alimentary reflexes, one reflex arc is formed as an result of association of a definite conditioned stimulus with food, as an unconditioned stimulus. The other reflex arc results from an association of another conditioned stimulus with the absence of food. Konorski thought that in the first instance there occurs an excitation of the hunger drive center, while in the other case the "hunger anti-drive center" is being excited (11, p. 323-329). When the animal is certain that food is not forthcoming, its response is similar to the kind of behavior observed during satiation, and according to Konorski, it has the nature of an excitatory response. The drive and anti-drive centers, however, are reciprocally connected by innate inhibitory links. As the conditioned response "reinforced" by food omission is being fixed, the conditioned response acquired by food presentation becomes more and more inhibited.

In their ultimate form, Konorski's views on inhibition essentially differ from Pavlov's conceptualization, as well as from his own earlier thoughts. Studies on the "primary inhibitor" conducted in the 1950's justified the usefulness of distinguishing inhibitory classical conditioned response as a separate variety of conditioned reflexes. But more than ten years later Konorski, in his initiations of anti-drive centers, generally undermined the division into excitatory and inhibitory conditioned reflexes. More precisely, it can be said that in his ultimate opinion the conditioning process is reduced to the establishment of only excitatory connections between neurons. The inhibition of conditioned reactions is a result of interactions between various reflex centers. Unlike Pavlov, who thought that the phenomenon of conditioned response extinction is a consequence of internal inhibition which develops within the conditioned reflex arc, Konorski arrived at the conclusion that the extinction of conditioned response is due to external inhibition, which is the effect of antagonistic interactions between different reflexes.

THE RELATIVITY OF DIVISION INTO CLASSICAL AND INSTRUMENTAL REFLEXES

What strikes one is the fact that 40 years after he had discovered the instrumental reflex theory, Konorski himself attenuated the importance of his discovery. In the postscript to his first publication, written for its English language edition of 1969, Konorski said: "Finally the sharp distinction between, not only the procedural side of type I and type II conditioned reflexes, but also between their physiological me-

chanisms seems to me now largely exaggerated. In fact, further investigation shows with increasing clarity that both types can be explained on the basis of the same general principles of connectionistic processes" (21).

Konorski presented that explanation in his monograph "Integrative activity of the brain" (11), where both classical and instrumental conditioned reflexes are considered as association systems acquired during ontogenetic development, and unconditioned reflexes — as symptoms of activity of innate association systems. An essential element of this reinterpretation was the analysis of various kinds of reflexes in the aspect of their biological role in the preservation or protection of the organism, subject to the general situation in which the organism remains. Among many divisions, the most interesting is the discrimination between consummatory and preparatory reflexes. The consummatory reflexes help in the immediate adaptation of the organism to actually active stimuli of vital biological importance, innate or acquired, as well as to unknown stimuli, especially those which appear unexpectedly. The preparatory reflexes, also called drive reflexes, serve to provide (or avoid) stimuli evoking consummatory reflexes. Originally drive reflexes were identified with instrumental reflexes, but Konorski in his last monograph was motivated by the need to separate not only the drive and consummatory classical conditioned reflexes (see the description of acquiring the hunger classical conditioned reflex, 11, p. 275 - 277), but also the drive and consummatory unconditioned reflexes (11, p. 8 - 39). Since under natural conditions various associations develop simultaneously, for instance an association between external stimuli and the drive they evoke and between the same external stimuli and the movement performed to satisfy the evoked drive, the elaboration of both classical and instrumental conditioned reactions is in fact parallel.

The fact that the conditioning processes are parallel does not mean that they are simultaneous. A careful analysis of processes used by Konorski and Miller in their early experiments shows that the essential element in reward training of the instrumental response is the transition from continuous to partial reinforcement of the classical alimentary conditioned response (31). This change brings about an excitation of the motor behavioral system, an increased attention to the environment and to stimuli acting upon the organism. The increase of the animal's motor activity is of an ordered nature. Subject to the animal's species and to its actual situation, various types of behaviors appear in a specified order and are performed with a different intensity. Among them appears that behavior which is a "condition" of food presentation. A few food reinforcements of the given motor response are sufficient to bring about

a radical change in the whole hierarchy of species-typical behaviors, and under given circumstances the reaction leading to food presentation will regularly appear. Then it can be said that an instrumental reflex has been developed.

The methods of developing individual varieties of classical and instrumental reflexes shown in Fig. 1 can be regarded as various kinds of relationships between the organism's reactions (including nervous processes which produce a given reaction) and the essential elements of the environment: the conditioned and unconditioned stimuli. In this conceptualization, conditioning is a process of discovering the specific organizing rules of these relationships and modifying the behavior accordingly, so that the vital needs of the organism are satisfied (33). The process is promoted by the state of activation of the motor behavioral system, which increases the probability of occurrence of various motor acts. Notably, every change in the organizing rules of the described relations (e.g. during extinction of conditioned reaction or during reversal learning) produces an increase of motor activity, especially an increased frequency of performance of the previously acquired instrumental response not only under conditioned stimulus, but also in the inter-trial intervals. Such performance of the instrumental response under atypical conditions, usually considered as the animal's error, accelerates the discovery of new relations between the organism's behavior and the essential elements of environment. It seems that the acquisition of new associations is facilitated not only by the activation of motor behavioral system, but also by the activation of afferent systems (see 11, p. 511–512). Physiological mechanisms responsible for the detection of relations between the organism's reactions and the essential elements of the environment are, however, far less known than mechanisms responsible for the performance of reactions in accordance with these relations.

THE RELATIVITY OF DIVISION INTO UNCONDITIONED AND CONDITIONED REFLEXES

Having analysed the development of Konorski's views on conditioning processes, one can form a conclusion of a gradual obliteration of differences between particular categories of adaptative reactions of the organism. This also concerns the division into inborn unconditioned reflexes and conditioned reflexes which are the effect of learning. Differing from Pavlov, Konorski stated in "Conditioned reflexes and neuron organization" that functional connections between nerve centers, which form the substrate of conditioned responses, can be established only if there certain previous "potential connections" resulting from the reali-

zation of genetic code in the ontogenetic development already existed between them (10). It follows that, subject to the degree of preparedness of the nervous system, the association between one pair of stimuli may be rapidly acquired, whereas the association between another pair of stimuli may develop with difficulty, and in some cases it may not develop at all.

The first experimental data confirming Konorski's hypothesis on the importance of potential connections for the conditioning process were obtained in the 1960's (6, 7). A food-reinforced instrumental response, putting the right paw on the feeder, was established in dogs. It appeared that, if the conditioned stimuli used to evoke the response was a tactile stimulus applied to the paw that performed the instrumental response, the training was several times shorter than with the use of auditory conditioned stimuli or of tactile stimuli applied to other body parts. A series of experiments was carried out to study the properties of a tactile stimulus applied to the extremity participating in the instrumental response, which has been called a "specific tactile stimulus". The responses to that stimulus had very short latencies, which persisted even in fully satiated animals (that did not touch food after they had performed the instrumental response), were highly resistant to extinction procedures and were restored almost immediately upon resuming the reinforcement of the instrumental response with food. Moreover, if the same instrumental response in a dog was trained to several various stimuli, the training of responses to the specific tactile stimulus led to a distinct attenuation of instrumental responses to the remaining stimuli.

Further research proved that the peculiar properties of the specific tactile stimulus result from the existence of innate connections between the sensory and motor area of the cerebral cortex (7). In the sensory area are localized neurons which represent tactile stimuli applied to body surface, and in the motor area three are neurons representing individual movements. The neurons of these two cortical areas are connected by U-shaped fibers running under the central sulcus (s. centralis). The cutting of these fibers totally eliminated the peculiar properties of tactile stimulus applied to the paw performing the instrumental response.

After surgery, that stimulus became similar to other conditioned stimuli in terms of the speed of acquisition of the instrumental response and its resistance to extinction, to the animal's satiation etc.

On the grounds of these studies Konorski expressed an opinion that the strength of a conditioned response depends on the combined action of direct connections between the conditioned stimulus center and in-

strumental response center, and of indirect connections between these centers running through the drive center. If the direct connections are very strong, as in the case of specific tactile stimulus, the instrumental response can be performed even with a very weak drive (e.g., when the animal is satiated). When the direct connections are weak, the dominant role in the realization of instrumental response is taken over by indirect connections and the dependence of the strength of response upon the drive level is clearly apparent (11, p. 427 - 432).

Further investigations showed that in many instances the strength of a conditioned response depends on the type of stimuli applied, the kind of reinforcement and the properties of evoked conditioned responses (32). The process of conditioned response training is subject to the biological properties of the organism investigated. These dependences are so essential that more and more is heard of biological limitations of the conditioning process, manifesting themselves, among other things, by the fact that the same task is solved differently by different organisms with the use of various connections between nerve centers.

"HOW DOES THE BRAIN WORK?"

In his autobiography (13) Konorski said that he had put this question to himself at the start of his career. During more than 45 years of research work he persistently sought to find an answer that would be as full and as true as possible. Nowadays thousands of laboratories throughout the world are engaged in research on the activity of the brain. In spite of great progress in brain research, the prevailing view is that no comprehensive theory exists which would explain the activity of the brain as an organ controlling the processes of the organism's adaptation to changeable conditions of the internal and the external environment (19). In many instances we are in an initial stage of the integration of facts collected by scientists working in various disciplines. This integration is being hindered not only by differences in methods, but also by totally different systems of concepts and terminologies.

I think that Jerzy Konorski's greatness shows in the fact that having formulated the instrumental reflex theory, he was not content with this achievement. For over forty years he worked continuously to lower the barriers between various disciplines dealing with brain research. He exposed the relativity of divisions between various categories of reflexes introduced by different schools in science, contributing thereby to earlier integration of results obtained in different research directions. His two basic monographs (10, 11) were attempts at such integration and they were successful attempts, especially when judged from a historical perspective. However, at the time of their publication they

brought no break-through. The resistance of various directions in brain research, represented by strong scientific schools, was too high. It is only now that the necessity of finding a comprehensive answer to the question "how does the brain work", fundamental to many disciplines, is properly appreciated.

The English version of the lecture delivered at the conference on the 10th anniversary of the death of Jerzy Konorski, held in Warsaw, 1 December 1983. The author acknowledges the careful checking of the English text by Dr J. F. Brennan.

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