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Review

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# Jerzy Konorski on brain associations

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**Abstract.** Jerzy Konorski (1903–1973) exerted a vital influence on the development of physiological psychology and neurobiology. Konorski and his friend and collaborator, Stefan Miller, distinguished instrumental conditioned reflexes as a separate type of acquired behavior, different from classical (Pavlovian) conditioned reflexes. In a series of pioneering studies Konorski demonstrated basic differences between the two types of conditioned reflexes. After the Second World War, he reinterpreted the results of research on conditioned reflexes on the basis of the mechanisms of Sherringtonian neurophysiology and introduced the term plasticity of the nervous system. His work, "Conditioned reflexes and neuron organization", published in 1948, signaled Konorski's place as one of the founders of contemporary neuroscience. He contributed significantly to the understanding of complex interactions of various classes of behaviors: innate and acquired, those driven by opposite motivations, and those elicited by cues signaling different contingencies. In his book "Integrative activity of the brain" (1967), Konorski analyzed the brain as a complex system directing the functioning of the organism as a whole.

**Key words:** learning, instrumental conditioning, plasticity, gnostic units, Konorski, Pavlov, Skinner

Editors' note: This manuscript has been submitted to ANE by Prof. Zieliński just one day before his death on January 10, 2004. It took us some time to decide what to do with the manuscript, as the Author could not improve it himself. Thanks to the invaluable help of Professors Robert Doty and Jim Brennan, the manuscript was streamlined and somewhat shortened, but the only person responsible for the ideas contained in the paper is Prof. Zieliński. Some eminent scientists offered their comments that are published following the paper. ANE thanks very much all those who took time to read, improve and comment the manuscript of Prof. Zieliński

## INTRODUCTION

Jerzy Konorski (1903–1973), the prominent Polish neurophysiologists and psychologist, contributed profoundly to contemporary theories of associative learning through conditioning, as well as to the complex brain mechanisms of perception, memory and motivation (Fig. 1). In 1921 he enrolled at the University of Warsaw where he studied mathematics, psychology, and finally transferred to the Medical Faculty. As students, Konorski and his friend Stefan Miller (1902–1941) were fascinated by Pavlov's theory of conditioning (c.f. Konorski 1974). Pavlov held a monistic view of the mechanisms of acquisition, execution and extinction of conditioned reflexes. The conditioned response (CR) was acquired as a result of a new association between an originally neutral stimulus paired with a more salient stimulus, which elicited an innate unconditioned response (UR), both manifested by the salivary response. Provided that the conditioned stimulus (CS) was consistently followed by the unconditioned stimulus (US) the CR was elicited regularly independently of the effector system involved. However, if the CS was no longer reinforced by presentation of the US, the CR gradually decreased and finally disappeared. The extinguished conditioned response may again be restored using the previous CS and US relations. The behavior executed by a trained subject during presentation of the CS has no influence on the occurrence of the US (Pavlov 1927).

Fig. 1. Jerzy Konorski (1903–1973). Picture by M. Holzman taken in 1971.

## INSTRUMENTAL CONDITIONED REFLEXES

The experiments of Konorski and Miller showed however that no motor learning occurs under conditions of the Pavlovian paradigm, where movements executed during the conditioned stimulus (CS) are without effect on the appearance of the unconditioned stimulus (US). Any specific motor response, e.g. leg flexion, is predicted from four different relations among the CS, the CR and the US. All of them were foreshadowed, investigated and described by Konorski and Miller in their first experimental paper (Miller and Konorski 1928, 1969). In reward training, a specific movement (e.g. right foreleg flexion) is a necessary condition for the appearance of an attractive unconditioned stimulus (e.g. food), whereas in omission training withholding the same motor response during the CS is a condition for appearance of an attractive US just after the CS terminates. In avoidance training, the specific motor response is a condition for not presenting the aversive US (e.g. electric shock), whereas in punishment training withholding the same response during the CS is necessary to prevent the aversive US action (Fig. 2).

Konorski and Miller called conditioned reflexes in which a specified overt behavior during the action of the CS was required to obtain a reward or to avoid punishment, conditioned reflexes of the second type (type II reflexes). In contrast, those discovered and investigated by Pavlov in which the CR did not produce any effect on the CS-US sequence, were referred to as conditioned reflexes of the first type (type I reflexes). These two types of conditioned reflexes are now called instrumental and classical conditioned reflexes after Hilgard and Marquis (1940) (see Kimble 1961).

According to Konorski and Miller instrumental and classical conditioned reflexes have to be considered as different types of learned behavior. Pavlov, who invited the two young investigators into his laboratory, was not

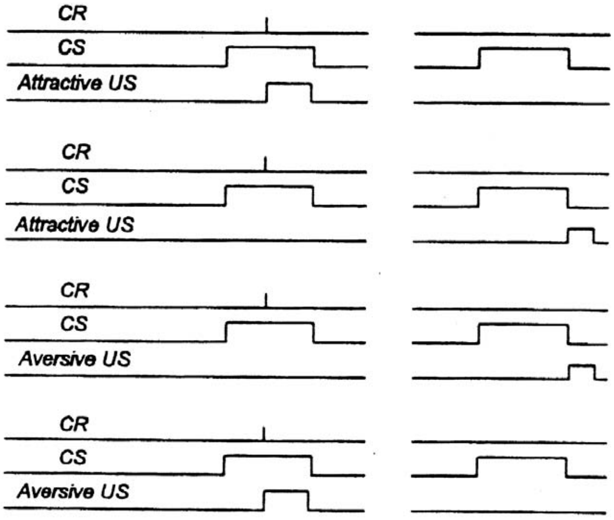


Fig. 2. Relationships between the conditioned stimulus (CS), conditioned response (CR) and the unconditioned stimulus (US) in various variants of instrumental conditioned reflexes. On the left are the relations between the CS and US when the CR is performed; on the right are the relations between the CS and US when the CR is not performed. The time course is from the left to the right in each graph. [Modified from Zieliński (1985)].

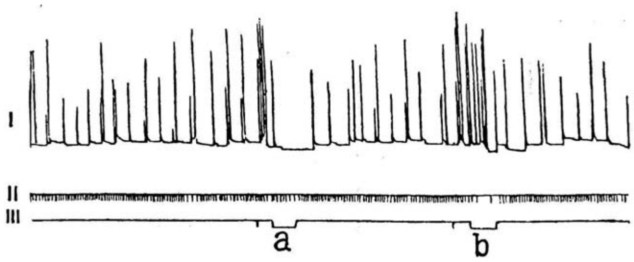


Fig. 3. An example of interaction of the classical conditioned stimuli: $CS^+$ (excitatory) and $CS^-$ (inhibitory), on instrumental responses performed in the experimental situation. Records from above: (I), movements of the hind leg; (II), salivation; (III), CS presentations. Note that the animal repeatedly lifted its leg. Each movement was reinforced with food. Marks in (III) show when the classical $CS^+$ (bell) rang for 15 seconds (a) or the $CS^-$ (metronome $M_{60}$) clicked (b). During presentation of both stimuli food was not given for a few seconds. Note that in response to $CS^+$ the dog immediately stopped performing movements waiting for food and salivating copiously. When the $CS^+$ terminated, instrumental responses reappeared. When the $CS^-$ was presented, movements were enhanced, but the salivation was much reduced. [Modified from Konorski and Miller (1936), p. 141].

convinced that the two types of conditioned reflexes should be distinguished. Konorski worked in the Institute of Experimental Medicine in Leningrad for two years (1931–1933), continuing his study of interrelations between instrumental and classically conditioned reflexes (Konorski and Miller 1933). The experiments confirmed the preliminary data obtained in Warsaw by showing that stimuli which elicit classically conditioned alimentary salivation exert an inhibitory effect on instrumental responses established by the food reward procedure. An original record from the Konorski and Miller paper (1936) illustrates this important finding (Fig. 3). Dogs used in the experiment were overtrained in classically conditioned salivary reflexes. Presentation of a sporadic auditory stimulus, a bell ring, had been consistently reinforced with food (an excitatory conditioned stimulus, CS+) whereas another stimulus, sound of a metronome, had not been paired with food (an inhibitory conditioned stimulus, CS-). In subsequent experimental sessions the CS+ stimulus was no longer used in the same experimental situation, but every spontaneous lifting of the right hind leg was reinforced with a small portion of food (reward training to the contextual stimuli). After stabilization of this instrumental response, a crucial test, which is now referred to as the summation, or combined-cue test (Dickinson and Pearce 1977) was used. Before the presentation of the original CS+ from the salivary conditioning stage, the food was not given for a few seconds despite repeated appearance of instrumental responses. As seen in the record, presentation of the CS+ immediately constrained these instrumental responses, whereas salivation was continued at a normal rate. In contrast, presentation of the classically conditioned inhibitory stimulus CS- reduced salivation and markedly enhanced the instrumental responses trained by the reward procedure (see also Konorski 1967, pp. 371–372).

These effects, which were not predicted by Pavlov's theory, demonstrated the basic difference between classical and instrumental reflexes. The demonstration that firmly established the effects of classically conditioned CS+ overshadow the contextual stimuli, which elicit the instrumental response, was subsequently confirmed by other researchers in experiments using the summation test (Dickinson and Dearing 1979, Hearst 1972). When the classically conditioned CS+ reliably predicts food, execution of the instrumental response is superfluous. The opposite response tendencies are elicited by the classically conditioned alimentary CS- and by the cue for the instrumental response based on reward training.

Many years later Konorski returned to the problem of the interrelations between the salivary and motor conditioned reflexes. He pointed out that in the usual instrumental training procedures the character of the CS is ambiguous (Konorski 1967, pp. 409–415). In order to evoke the instrumental response, the CS has to elicit the preparatory drive reflex assisting in providing attractive stimuli (or in preventing the appearance of the aversive stimuli). However, when the alimentary instrumental response has been established by the reward procedure, the CS is always reinforced by food with a short CS-US interval and therefore becomes a strong type I food CS manifested by salivary response. In order to separate the instrumental and the classical aspects of the CS, an experimental set-up has been designed in which the instrumental motor response was not contaminated with the classical salivary response (Ellison and Konorski 1964, 1965). Two distinct conditioned stimuli were presented in succession. A fixed ratio of lever press responses during one CS was required for bringing up another CS of another modality, which was followed by food. The first CS (type II CS) produced a general motor excitement of the dog and repeated lever pressing, whereas salivation was depressed or absent. In contrast, during the next CS (type I CS) the dog calmed down, stared at the feeder and salivated copiously. Thereby, a separation of the instrumental CS driven by hunger and the classical food CS has been achieved.

Mowrer (1976) and Dickinson (1992) suggested that the existence and the importance of the distinction between the classical and instrumental conditioned reflexes was not realized in the West until Konorski and Miller entered into a published debate with Skinner. The theoretical papers were published in the Journal of General Psychology in 1935 and 1937 (Konorski and Miller 1937a,b, Skinner 1935, 1937). The disagreements concerned the mechanisms of the new type of reflexes.

The positive results of this theoretical dispute were manifold and included a reformulation of the position outlined by Skinner in the paper initiating the discussion, and the introduction of the terms “operant” and “respondent” behaviors. More important was refinement of the terms “reflex” and “response”. In these years it was not always clear whether these terms mean the basic structure of the complex chain of neural processes or only their final link, the observable behavior. During the debate Konorski and Miller proposed that reorganization of the central part of the neural network was a prerequisite for formation of the new reflex. The occurrence of an overt response was of lesser importance. After years, Konorski agreed with Skinner that the passive movements method employed by him in early experiments cannot be instrumentalized, unless it included reflex elements (see Konorski, 1967, pp. 467–470, Miller and Konorski 1969).

## ROLE OF INHIBITION IN CONDITIONING

The problem of conditioned inhibition occupied a central position in the theory of instrumental conditioning developed by Konorski (see Zieliński 1976). According to the conditioning-extinction theories of Pavlov, and of Spence and Hull, both the tendency to respond and the tendency not to respond are results of conditioning. Pavlov distinguished two basic situations in which a learned response may be suppressed independently of changes in motivation, fatigue, or adaptation. If a new stimulus is presented concurrently with a CS, it may evoke its own unconditioned reflex (e.g. an orienting reflex), and as a result of a competition between the two reflexes, the CR may be partially, or even totally inhibited. Pavlov termed the interfering stimulus as an external inhibitor, in order to stress that the arc of the conditioned reflex was intact, but the response was inhibited as a consequence of excitation of other nervous centers. The second situation under which a conditioned response is suppressed involves a change in the relationships between the CS and US (Pavlov 1927). Such a change may be caused by a cessation of US presentation following the CS (extinction), or by an increase in the time interval between the onset of the CS and US (inhibition of delay), or when US does not follow a new stimulus, which is different from the original CS, but receiving generalized excitation (differential inhibition).

According to Konorski (1948), a stimulus repeatedly presented without a reinforcement signals that no biologically important change in the environment will follow this stimulus. During extinction of an excitatory response, the positive correlation between the CS and the reinforcement changes to a negative correlation and not to the lack of correlation. In the inhibition of delay paradigm the early phases of the CS, remote from the US, undergo a process of experimental extinction, whereas the late phases of the CS retain their excitatory properties. Konorski was the first to publish in English an extensive review of the Pavlovian theory of inhibition involved in conditioning, together with his own critical comments (see Konorski 1948). The importance of the problem of inhibition in learning was generally not recognized until the 1960's, when Konorski's idea of excitatory-inhibitory interactions during conditioning was incorporated into contemporary theories of conditioning (see Dickinson and Dearing 1979, Hearst 1979, Rescorla 1967).

Interrelations between different types of conditioned reflexes were repeatedly considered by Konorski. Both antagonistic and synergistic relationships were observed between various conditioned stimuli, e.g. stimuli signaling instrumental and classical conditioned alimentary reflexes based on the same UR, as revealed by the above mentioned summation test (see Konorski and Miller 1936).

On the basis of their studies, Konorski and Miller explained that during instrumental alimentary conditioning the classical and instrumental reflexes are acquired separately although simultaneously. Extending their analysis to classically conditioned fear and instrumental avoidance response they revealed an important modulatory role of fear in instrumental defensive conditioning. Thereby they formulated an early version (see Dickinson 1992) of the two-process theory of defensive conditioning developed further by Mowrer (1947), Solomon and Wynne (1953) and Rescorla (1967).

One of the topics of particular interest for Konorski was that of the discrimination and differentiation of conditioned stimuli and responses evoked by them. Konorski considered discrimination as a purely perceptual process and the differentiation denotes the utilization of discriminated stimuli for different responses of the organism (compare Konorski 1967, p. 93).

Konorski used the following example to illustrate the difference between detecting the information and using this information. A dog with a well trained classical conditioned alimentary reflex reacts to the CS, e.g. a tone of a definite frequency, by secreting a rather stable amount of saliva. Presentation for the first time of a tone of a different frequency is followed by a much weaker salivation as a result of the orienting response, and indicates that the animal immediately perceives the change of the stimulus (Konorski 1962). After a number of trials in which the new tone is presented without any food, at first the amount of salivation starts to increase due to generalization of excitation from the earlier frequency, indicating a process of habituation of the orienting response to the new tone. Only later, when the new stimulus is still repeatedly presented without reinforcement, the salivation evoked by it finally decreases. Thus, the utilization of the perceived change between the stimuli for adjusting the salivary responding occurs much later than noticing the change (see also Rescorla 1979).

The above example illustrates the course of events during Pavlovian differentiation learning which consists of contrasting two classically conditioned reflexes. The mechanism of differentiation learning is the same whether attractive or aversive unconditioned stimuli are used.

Differentiation learning involving instrumental responses included many more variants. In this case, any conditioned reflexes, be they instrumental or classical, evoked by a specific CS may be opposed to each other. This may be illustrated in a situation in which an alimentary US and two discriminable CSi are presented on separate trials, in which a specific motor response is required as a reaction to one CS, whereas the animal should not react to the other CS ("go, no-go differentiation"). During differentiation of alimentary instrumental reflexes, a specific movement in response to the CS+ is necessary for obtaining food. Thus, the reward training has to be used during positive trials. During negative trials two different procedures are possible. The CS- may never be paired with food or, on the contrary, the correct response to the CS- (lack of a specified movement) would be required and reinforced by food after the CS- is terminated. The first procedure has been termed "go, no-go differentiation with asymmetrical reinforcement" and corresponds to the original procedure of Konorski and Miller who applied the classical inhibitory conditioned reflex on negative trials (Konorski and Miller 1933, 1936). The second procedure was originally used in some experiments on monkeys by Weinskrantz and Mishkin (1958) and has been termed "go, no-go differentiation with symmetrical reinforcement" (Zieliński 1976, 1979). In the "symmetrical" procedure, two different varieties of instrumental reflexes were used: reward versus omission training. Despite similar behavioral outcome of the two procedures, the results were achieved via different neuronal circuits, since selective prefrontal cortical lesions in the dog affected the asymmetrical and symmetrical differentiation tasks in opposite ways (Dąbrowska 1971, 1979). In Pavlov's laboratories Konorski demonstrated that in omission training the instrumental stimulus elicited the active movement of pressing the floor of the stand according to the force applied by an experimenter to shift the leg from a position (Konorski and Miller 1936, pp.198–202).

Associative learning is highly adaptive because it provides an animal with the ability to discover relationships between biologically important events, which are not sufficiently predictable or are too detailed to be encoded genetically (see Gould 1984). Variants of classical and instrumental reflexes may be regarded as the means of discovering the specific organizing rules of the relationships between the organism and the environment and modifying the behavior in such a way that the vital needs of the organism are satisfied. The process of learning is greatly promoted by a general activation of motor behavioral systems which increases the probability of occurrence of the appropriate motor reactions. The original procedure of instrumental training involved two kinds of random trials. In some of trials the leg of a dog was passively flexed during presentation of the future CS and rewarded with food, while in other trials the same CS was applied without leg flexion and without food. Thus, the continuous reinforcement schedule was changed to a partial food reinforcement schedule (see Zieliński 1979). In trials without reward a marked enhancement of motor excitement was observed and an increasing frequency of leg flexions accompanied other movements. Under these conditions an increasing number of active leg flexions could thus be rewarded with food, allowing a rapid fixation of the instrumental response. Konorski indicated that motor learning is facilitated not only by the excitation of the motor system, but also by activation of afferent systems (Konorski 1967, pp. 393–403).

## NEURAL BASE OF CONDITIONING

After reactivation of the Nencki Institute of Experimental Biology at 1945, Konorski organized the Department of Neurophysiology which he headed until the end of his life. His monograph, "Conditioned reflexes and neuron organization", was published in 1948 by Cambridge University Press. The central message of the book was that morphological changes in neuronal synaptic connections should constitute the substrate of learning. Plasticity of the nervous system, or parts of it, was defined as the ability to undergo relatively permanent structural changes due to information processing (Konorski 1948, pp. 79–80). In contrast to excitability, which is an inherent property of nerve cells in the entire nervous system, Konorski expected plasticity to be manifested mainly at the highest levels of the nervous system, especially within the cerebral cortex of the brain. In contrast to Pavlov, Konorski proposed that functional connections between nerve cells, mediating CRs, can be established only on the basis of the pre-existing "potential connections", formed as a result of the expression of the genetic program during ontogenesis (Konorski 1948, p. 87). Potential connections were considered as already existing anatomic pathways which were not used for various reasons.

The first experimental data relating instrumental reflexes to such potential connections were soon obtained. A dog was trained to put its paw on the feeder for reward. Learning was considerably faster when a tactile stimulus applied to the trained paw was used as a CS, than when auditory stimuli or tactile stimuli to other body parts were used. Instrumental responses to a tactile stimulus applied to the extremity "specific tactile stimulus" (STS), which were performed at very short latencies and persisted even after satiation, were highly resistant to extinction, and restored almost immediately upon the resumption of food reward. Moreover, after introduction of the STS stimuli after the instrumental response has been established to "regular" CSi, the instrumental responses to other stimuli were greatly attenuated (Dobrzecka and Konorski 1962).

The peculiar properties of the STS were related to much stronger and more direct pre-existing connections between the sensory and motor fields of the cerebral cortex than between other cortical areas. Cortico-cortical connections between areas of the somatosensory cortex and motor cortex (MI) arise from the neuronal population in layers II/III and less numerous in layers V/VI. Surgical damage of these fibers resulted in a total elimination of the unique properties of the STS. After a lesion of these fibers the properties of STS became similar to those of other CS in terms of the rate of acquisition, latency of the CR, resistance to extinction and satiation (Dobrzecka et al. 1965).

Konorski also demonstrated a marked differences in the ease with which animals differentiated various stimuli in two kinds of differentiation tasks. When allowed to use directional cues provided by auditory stimuli, dogs and monkeys easily mastered a spatial differentiation while the same task was solved with great difficulty when auditory stimuli differed only in frequency. In contrast, the go, no-go differentiation was easy with frequency cues and very difficult when stimuli differed only in their location. Moreover, when both parameters were simultaneously available (the stimuli differing both in their frequency and location), the animals ignored either the localization or the frequency depending on the differentiation task (Dobrzecka et al. 1965, Ławicka 1964). Konorski's concept of "potential connections" anticipated discussions on constraints of conditioning (LoLordo 1976) and on selective associations (Shettleworth 1976).

## RULES FOR CHANGING OF SYNAPTIC CONNECTIONS' WEIGHTS

If one accepts that any plastic changes in the brain are based on pre-existing connections between neurons, the main problem of the theory of conditioning must be to explain how connections between neurons are being changed. This was the main question addressed by Konorski in 1948 in his monograph, "Conditioned reflexes and neuron organization", in which he formulated the following set of hypotheses.

1. The prerequisite for forming a conditioned reflex is the existence of potential connections between cortical neurons receiving information about the stimulus that will be conditioned (the "emitting center") and neurons receiving information about the US (the "receiving center").

2. When excitation of the first center coincides in time with an increase in excitation of the second center, the potential connections between them are transformed into actual excitatory connections.

3. Inhibitory connections are formed when the excitation of an emitting center, coincides in time with a decrease in excitation in a receiving center.

4. "The plastic changes would be related to the formation and multiplication of new synaptic junctions between the axon terminals of one nerve cell and the soma (i.e. the body and the dendrites) of the other" (Konorski 1948, p. 89).

5. The repetition of a certain combination of stimuli giving rise to a definite plastic change leads to an increase in the response to these stimuli. The accumulation of plastic changes depends on the number of repetitions of the combinations of stimuli (i.e. trials) and also on the intervals between trials.

With respect to the proposed inhibitory mechanisms, Konorski stressed that the CS given without the US represents a particular combination of stimuli and must therefore lead to the formation of new plastic changes in the cerebral cortex, but without eliminating the old ones. He proposed therefore "that non-reinforcement of a conditioned stimulus by an unconditioned stimulus causes formation and multiplication of new synaptic connections of an inhibitory character side by side with old ones" (Konorski 1948, p.134).

The new theory of conditioning based on changes in synaptic connection weights outlined in Konorski's book was probably overshadowed by the extensive critical review of Pavlov's theories. Most of the reviewers of the "Conditioned reflexes and neuron organization" emphasized therefore its critical aspects. However, the importance of his proposals was quickly recognized, e.g. by Adrian (1949), Hebb (1949), and Eccles (1964). Nevertheless, the new theory of conditioning raised considerable irritation at that time in the Soviet Union and some repercussions in Poland (Scientific conference 1952). Much effort and courage by Konorski and his friends from the Nencki Institute were needed to defend the neurophysiological and neurobiological approach in studies of conditioning and learning.

Konorski remained fairly isolated from the main stream of world science for almost a decade. The situation changed with political events in 1956. The next year Konorski visited many scientific centers in USA, and started close collaboration with several groups of neurologists and neurophysiologists (see Konorski 1974). These projects focused primarily on functional and morphological organization of the prefrontal cortex and on its involvement in inhibitory control of alimentary drive functions and in memory (Konorski et al. 1972).

## INTEGRATIVE ACTIVITY OF THE BRAIN

The results of experimental and theoretical studies on neural substrates of learning carried out by Konorski and his collaborators were summarized in his next monograph, "Integrative activity of the brain" (1967), which was centered on problems of perception and motivation. In the monograph Konorski introduced the concept of gnostic units, as the main category of unitary perception. He emphasized the important role of lateral inhibition in perceptual processes at the highest levels of the nervous hierarchy. Konorski assumed that at a sufficiently high level within the analyzer system, unitary perception was mediated by discharge of a set of gnostic units or even a single neuron. The gnostic units correspond to biologically meaningful stimulus patterns used in behavioral associative processes (Konorski

1967, pp. 73–76). According to his proposal, neurons at the lowest levels of all afferent systems have primarily receptive functions while neurons at successively higher levels integrate elements of information which extends them into more and more complex patterns, single elements of information provided by particular receptors being lost in this process (see Gilinsky 1969, John 1975).

Konorski based his proposal of gnostic units primarily on the subdivision of the cerebral cortex into distinct perceptive and associative areas, the wealth of intercortical connections, and on clinical observations that different deficits are caused by lesions of the various cortical areas, and that electrical stimulation of the cortex during neurosurgical operations may give rise to definite perceptions. Furthermore, Konorski postulated that gnostic units (or patterns of information that they integrate) are a product of a learning process. Once a potential gnostic unit has been occupied by the particular stimulus-pattern and thus transformed into the actual gnostic unit, the unit would be resistant to any new stimulus-patterns (Konorski 1967, p. 90).

Gross (2002) underscored the pioneering role of Jerzy Konorski in predicting the existence of highly specialized perceptual neurons in mammals, sensitive to complex stimuli such as faces, hands, emotional expressions and animate objects. Konorski's views on the neural organization of perception have been considered as a synthesis and extension of Hubel and Wiesel's demonstration of the hierarchical processing of sensory information and was itself the result of a long-lasting collaboration with Hal Rosvold and Mortimer Mishkin from NIH, who showed that lesions in the inferior temporal cortex produced specific impairments in visual cognition in monkeys. Konorski's important role stemmed from his deep interest in the physiological mechanisms of aphasia and his familiarity with various agnosias that follow cortical lesions and disconnections between gnostic fields in humans (Gross 2002).

Another important subject from the "Integrative activity of the brain" is Konorski's treatment of inhibitory reflexes (Konorski 1967, pp. 316–329). Changing his earlier view, he came to the conclusion that inhibitory CRs are the effects of interactions between two arcs of excitatory conditioned reflexes. In the case of alimentary behavior one reflex arc is a result of an association of a certain CS with the food US. The other reflex arc is a result of an association of another CS with the absence of food. The first CS contributes to the excitation of the hunger drive center, whereas the second CS excites a hunger anti-drive center, the drive and anti-drive centers being reciprocally connected by innate inhibitory links. According to Konorski an animal informed that no food will be given behaves in a similar way as when it is satiated, and therefore its behavior may be classified as an excitatory response. Based on the experimental data of Konorski and his coworkers, he introduced new terms. He noted an important role of the history of a stimulus on its actual associative properties. A stimulus consistently presented without reinforcement in a situation in which a given unconditioned activity (alimentary, defensive, and so on) is displayed, was called a "primary inhibitory stimulus", whereas a stimulus which was previously a positive CS, but has lost its meaning by extinction training, was called a "secondary inhibitory stimulus" (Konorski 1972, see also Konorski 1967, p. 320). These important implications of this new model have been described elsewhere (see Bignami 1968, Rescorla 1979).

By extending his conclusions on the interrelations between the hunger drive and anti-drive centers to other drives, Konorski started to consider the antagonistic interactions between opponent neural processes as one of the main principles of integration of motor activity (cf. Gilinsky 1969). Konorski used this principle to explain why it is easy to convert an alimentary CS- into a defensive CS+, or *vice versa*, but very difficult to convert an alimentary CS+ into a defensive CS+, or *vice versa* (Konorski 1967, pp. 323–329). Konorski and his coworkers showed that the extinction and restoration of the CR related to the same drive (e.g. hunger), are based on the same principle as are transformations of any antagonistic heterogeneous conditioned reflexes. This concept became soon quite popular among other researchers (see Dickinson and Dearing 1979, Hearst 1972, Rescorla 1979, Zieliński 1976). According to Konorski, drives are the mechanisms controlling the preparatory CRs (referred also to as drive reflexes, i.e. the instrumental or type II reflexes according to his earlier terminology), and the emotions are their psychological counterparts.

Block diagrams of relationships between drives and various kinds of reflexes presented in his last published paper illustrate his final view on the connections between centers operating in classical and instrumental conditioning. The final conclusion presented in this paper was that the only difference between classical and instrumental conditioning lies in a different circuitry of connections formed between particular centers, due to different experimental procedures. In classical conditioning the CS regularly precedes the US; and therefore, the connections are formed between the CS center and the US center under the influence of drive, which produces arousal of these centers. In instrumental conditioning the CS regularly precedes the given movement, and therefore the connections are formed between the CS center and the kinesthetic center of the movement (Konorski 1993, pp. 6–8).

In this way Konorski brought together two of his fundamental discoveries: the distinction between the two types of conditioned reflexes presented for the first time in 1928, and the rules for changing neuronal synaptic connections formulated in the "Conditioned reflexes and neuronal organization", published in 1948.

## CONCLUDING REMARKS

Konorski's ideas on the mechanisms of learning were shaped during a period extending over 45 years and underwent continuous evolution. One of the main factors contributing to the evolution of these ideas was results of the research carried out by himself and by his colleagues. Another, and perhaps even more important factor, was the very rapid development of neurobiology during his lifetime. When he started his research, the ideas about the nature of either excitatory or inhibitory processes were only vague, while the last years of his life coincided with an overflow of detailed information about synaptic processes not only at a cellular, but also at subcellular levels. Therefore it is not surprising that Konorski modified not only the terminology he used to describe the two types or conditioned reflexes (from type I and II, through classic and instrumental, to consummatory and preparatory or drive reflexes), but also took into account an increasing number of neural mechanism to explain the differences between them.

Starting from the traditional approach and definite varieties of classical and instrumental conditioning in terms of experimental paradigms, Konorski consequently changed his conceptualization referring learning processes to the functional cortex. His book "Integrative activity of the brain" (1967) has to be considered one of the early attempts to consider the perceptual-motor organization of motivational processes underlying behavior organized into functional systems developed under evolutionary selection pressure (see Timberlake 1994).

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# Comments

## THOUGHTS ON JERZY KONORSKI

I first met Jerzy Konorski when he visited Clinton Woolsey's laboratory of neurophysiology at the University of Wisconsin, in, I believe, 1957. At that time I was a post-doctoral fellow in Woolsey's lab, having received my Ph.D. in Psychology from the University of Wisconsin in 1956. I was assigned the task of hosting Professor Konorski during his visit, perhaps because of my background in psychology and deep interest in learning and memory.

I remember so clearly that Jerzy (I of course addressed him then as "Professor Konorski") was intense and indefatigable. At that time I was young and in very good health (I swam several miles a week). Yet just keeping up with Jerzy left me totally exhausted. He was intensely interested in all the work ongoing in Woolsey's laboratory, particularly as it might relate to processes of learning and memory. A major focus of the laboratory was on somato-sensory and somato-motor areas of the cerebral cortex and their interconnections, of particular interest to Jerzy because of his work yet to be done on STS (see Dobrzecka and Konorski 1962, Dobrzecka et al. 1965).

I was of course strongly influenced by Konorski's ideas in my own career, having read his monumental 1948 and 1967 books. Konorski's fundamentally important distinction between what we now call classical and instrumental conditioning or learning (Konorski and Miller 1937a,b, Miller and Konorski 1969) was a major departure from Pavlovian dogma of the time. It must have been very difficult for the young Konorski in the late 1930s to challenge the dogma. Pavlov was held in very high esteem not only in the Soviet Union, but also in Poland. Consequently, it must have taken a great deal of courage for two young students, Konorski and Miller, to challenge his views.

The last half century of research on brain bases of learning and memory really constitutes a major verification, indeed vindication, of Konorski's ideas. It is now clear that basic forms of classical conditioning and instrumental learning involve very different brain systems. The classical conditioning of discrete movements (eyeblink, limb flexion, etc.) critically involves the cerebellum (our work, see Christian and Thompson 2003, Thompson 2005) and classical conditioning of fear critically involves the amygdale (see Fanselow and Poulos 2005). In marked contrast, instrumental learning critically involves the hippocampus and cerebral cortex (Squire 2004). I realize that Konorski placed greater emphasis on the cerebral cortex in his neuronal theories of learning, but his fundamental distinction between instrumental and classical conditioning has proved to be instantiated by the brain in terms of different brain systems.

Another major contribution of Konorski's thinking is the notion that functional connections between nerve cells mediating CRs "can be established only on the basis of pre-existing 'potential connections,' formed as a result of the expression of the genetic programs during ontogenesis" (Konorski 1948, p.87 – see Zielinski's review). In our own work on classical conditioning of discrete responses, e.g., eyeblink, this has proved to be precisely correct. The region of the cerebellar interpositus nucleus critical for the conditioned eyeblink response is in fact the motor representation of the eyeblink in the interpositus. Before training the connections from the CS pathway (e.g. tone) to this higher order motor program are much too weak to elicit the response, but after training the connections from mossy fibers to interpositus neurons become much stronger, indeed new synapses in this already existing pathway are formed as a result of training (Kleim et al. 2002). Consequently the tone now elicits the conditioned eyeblink response (see Christian and Thompson 2003).

Konorski is a towering figure in the intellectual history of learning and memory in the 20th century. It is most fortunate that he received the accolades he so richly deserved while he was still alive.

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## KONORSKI'S INFLUENCE ON CONTEMPORARY NEUROSCIENCE

I first met Jerzy Konorski during his visit to the laboratories of Horace Magoun and Donald Lindsley in the Brain Research Institute at UCLA, which was his first visit to the US. At that meeting we began an intense discussion that continued whenever Jerzy's travels brought him to the US and whenever I found the opportunity to visit Warsaw. We viewed the brain from two very different vantage points: Jerzy from his innumerable ingenious conditioning experiments and his studies of the behavioral effects of brain lesions and I from observations of brain electrical activity including the EEG, evoked potentials and single unit activity in different brain regions during behavior by unrestrained animals. In hours of intense and enjoyable discussions, we tried to reconcile these two very different databases. In the many years since then, I have seldom met a man more dedicated to the objective pursuit of understanding with complete open-mindedness and no encumbrance by personal egotism.

As neuroscience has moved away from the focus on the neural mechanisms mediating conditioned behaviors and toward the analysis of cellular neurophysiological mechanisms on the one hand and the system analysis of cognitive processes in humans using gross brain imaging techniques on the other hand, there are two areas in which Jerzy's conceptualizations continue to be most relevant. His early conclusions that learning must lead to the formation and multiplication of new synaptic connections and his proposal that successive convergence within analyzer systems logically must lead to mediation of unitary perceptions by discharge of a set of Gnostic units or even a single "grandmother cell" were the forerunners of research endeavors that continue until the present day. Unfortunately, there has been little recognition that these contributions largely foreshadowed Hebb's formulation of cell assemblies and Hubel and Wiesel's identification of neurons sensitive to specific stimulus attributes arrayed into complex and hypercomplex hierarchies, and there is little acknowledgment of his pioneering role.

Personally, I believe that these concepts of Jerzy are only a part, albeit an essential part, of how adaptive behavior is attained. While abundant evidence has shown that synaptic changes in neurons and alterations among functional neuronal interconnections undoubtedly occur with experience, these cellular changes are not stable but evolve continuously. Abundant evidence exists of highly specialized neurons in mammals, sensitive to the perception of complex stimuli such as faces or particular objects. Yet, dynamic brain imaging studies are providing growing evidence that perceptual processes are mediated by interactions among sets of highly synchronized neurons within huge neural ensembles in widely dispersed brain regions. This implies that the activity of a single neuron may be relevant to perception only insofar as it contributes to statistically significant synchronous oscillations binding together these large ensembles.

It is a great loss that the brilliant insights of Jerzy Konorski are no longer available to help the neuroscientific community to reconcile these apparent contradictions between the unitary properties of the elements comprising the system and the global properties of the system as a whole.

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## KONORSKI'S INSIGHTS AND PERSONALITY

How sad it is, and disappointing to me personally as one of his many students, that Jerzy Konorski did not have nearly the impact on integrative neuroscience that he deserved to have at the time he wrote his two books. And these, on top of his discovery with S. Miller of 'Type II', or instrumental, conditioning. In a way, his star was dimmed by an unfortunate accident of geopolitics. Had he lived in the west, I am certain his star would have shone far, far brighter than it did. By now, many of his ideas, though remarkably creative and forward-looking at the time, have been rendered a bit archaic by all the integrative neuroscience research that has been conducted since his two books were written. The first one, a groundbreaking application of Sherrington's neuronal theory of spinal cord mechanisms for understanding cerebral function, predated D.O. Hebb's adoption of the same idea. And his second book, a masterly psychoneurological analysis of both innate and learned behavior and cognition, can still be mined for the many uncanny insights it contains. Those of us who knew first-hand his exuberant dedication to brain science and his brilliant contributions to it cherish the memory of an unpretentious man with the stature of a giant in our field.

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## REFLECTIONS ON ZIELINSKI IN LIGHT OF HIS COMMENTS ON KONORSKI

Prof. K. Zielinski in the spring of 1993. Photo by W.J. Wilson.

It is fitting that Zielinski's final paper is an examination of Konorski's contributions to our understanding of learning: were it not for Konorski's approach to learning (both at theoretical and methodological levels) Zielinski's scientific career would almost certainly have followed very different directions. Konorski's discovery of instrumental learning (with Stefan Miller in 1927) complemented Pavlov's "Type 1" conditioning and created a novel Polish school of learning that fostered some great scientific careers, including that of Zielinski. Of his students, Zielinski perhaps was closest to Konorski in style if not in substance; herein I will share some personal reflections on Zielinski the man and Zielinski the scientist.

I spent 6 months in the spring of 1993 on sabbatical at the Nencki Institute, working in Zielinski's Laboratory of Aversive Conditioning. Zielinski was a gracious host and strong scientific mentor. This was my first experience with the European model of a scientific hierarchy (far more formal than its American counterpart) and "the Professor" was very forgiving of this sometimes-too-informal American. When I was behind some equipment and needed someone to take a cable out of my hand, I said, "Kazik, will you please take this wire?" Jaws dropped among the other Polish scientists in the room (that is, they were shocked at my lack of formality) but he took it in good stride (apparently used to informal Americans). Having said this, though, it was always clear that Professor Zielinski was a very proper Polish scientist, both expecting and deserving respect.

Like Konorski, Zielinski was highly empirically oriented, always going to the data for answers. A story is told about Konorski by his family that when he was young he was so nearsighted that he could not see the stars, and he refused to believe in them until he saw them when he got his first glasses (personal communication from Konorski's great-nephew, also named Jerzy Konorski). It was a common experience in Zielinski's laboratory or office to find him poring over data, drawing graphs or calculating statistics in an effort to learn something new. He was not content to see the results of an experiment from his laboratory after others had summarized or analyzed the data; he wanted to see the raw data such that he could draw his own conclusions. (And to determine that the mushrooms that he collected in the forests near Warsaw were safe to eat, Zielinski insisted on empirical evidence as well: he told me that upon collecting new mushrooms he always invited a particular friend, a mathematician, to dinner. If the friend suffered no ill effects, he knew that the mushrooms were safe.)

Zielinski also insisted on watching his animal subjects. A common trend among researchers studying animal behavior starting in the 1960s has been to automate behavioral equipment, yielding a stream of abstract data reflecting the animal's behavior, which no longer needed to be observed directly. Yet despite automated equipment, Zielinski still wanted to watch. During my time at the Nencki Institute in 1993 he was very proud of the video cameras that allowed him to watch the rats in their chambers. He wanted others to observe the behavior as well, and not to be satisfied with the stream of abstract data. I worked with Zielinski on a study of two-way avoidance (Zielinski et al. 1993) in which the data that we needed were recorded by a computer. Nonetheless, Zielinski insisted that someone (one of us or a technician) watch the rats on a video monitor placed beside the computer screen. On occasion (perhaps on average once every 10 minutes) the computer would stop controlling the session and instead displayed a small box that said “Press a key to continue” (or something to that effect); I do not recall whether this message was displayed in English or Polish, but most likely it was in Polish. When a key was pressed the session would resume. Zielinski complained to me whenever this message appeared that nearby construction must be interfering with the computer's function. I expressed incredulity at this explanation, convinced (and perhaps Tomek Werka might confirm this) that Zielinski had arranged for the computer program to function exactly as it did. I maintain, in the absence of any evidence, that Zielinski wanted to ensure that someone was always present and observing while the behavioral data were collected.

With regard to Zielinski's thoughts about the importance of Konorski's work as detailed in his last paper, I have two comments. It is clear that Pavlov had considered contiguity sufficient for learning to occur; beginning in the 1960s this view was changing and the predictive value of the CS was becoming paramount. Rescorla's (1967) insistence on the truly random control, for example, was driven by the realization that only when a stimulus had zero correlation (and thus no predictive value) with regard to a US would it not be associated with the US (in either an excitatory or inhibitory manner). The change from the contiguity to the predictive model of Pavlovian conditioning required an appreciation of the importance of inhibition – an importance that was far more fully developed by Konorski than by anyone prior to him. Zielinski is correct to point out the significance of Konorski's work on inhibition.

Zielinski also points out some contributions made by Konorski in the realm of the neural bases of behavior. For example, Zielinski addresses the importance of Konorski's ideas about changes in synaptic strength resulting from experience. The “Hebbian synapse” is known to most students of the physiology of learning, but Buzsaki pointed out to me that Konorski's explication of the mechanism was far clearer and more complete than Hebb's so much so that Buzsaki insists on referring to the rule governing this strengthening of synapses as the “Hebb-Konorski rule” (personal communication, 2003). That Zielinski highlights this contribution is further evidence of its centrality.

Konorski's “gnostic units” represent an independent formulation of what have become known in the West as “grandmother cells”. Zielinski appropriately cites Gross (2002), who pointed out Konorski's role in this matter. It is perhaps unfortunate that Lettvin (see Gross 2002) is typically credited alone as the originator of the grandmother cell concept. Clearly Zielinski was correct to cite gnostic units as one of Konorski's lasting contributions.

Zielinski's early scientific career was spent in Konorski's shadow. An examination of his work after Konorski's death in 1973 reveals that he left the shadow and developed his own sense of self as a scientist. He added to our understanding of behavior, and he will be missed.

I thank the editor for the opportunity to contribute these thoughts, and Professor Zielinski for the hospitality that he provided during two visits to the Nencki Institute. The reader can contact me via email at wjwilson@albion.edu.

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## CHANGING PARADIGMS, CHANGING GENERATIONS

I was pleased to read an early draft of Prof. Zieliński's paper, "Jerzy Konorski on brain associations", and work with my colleagues on Acta Neurobiologiae Experimentalis in bringing this work to print posthumously. The topic of this paper, along with some earlier versions dealing with the same developments, was long a preoccupation with Prof. Zieliński. He believed strongly in the gradual shift in paradigm within associative learning, instigated in the 20th Century through the work of Sherrington and Pavlov. Konorski's research and writings were essential in this development, and the contextual importance for Polish neuroscience plays a central part of the story.

The paper itself represents a sweeping summarization of a thematic progression starting with the seminal paper of Konorski and Miller and further developed in several representations of the historical dual processes underlying Classical and Instrumental Conditioning. The series of experiments studying excitatory and inhibitory differentiation, emanated from the programmatic vision of the reconstituted Nencki Institute following World War II, represented an amazingly productive output under often adverse situations. Yet, consistently over this period, a programmatic framework for associate learning emerged, adding compelling evidence of the recovery of Polish science.

As this research productivity continued and evolved after Konorski's death in 1973, the place of his colleagues and students in the triumph of late 20th Century neuroscience was certainly prominent. It saddens me that with Prof. Zieliński's passing, the insights from this exciting period in the emergence of brain science pass from that of first-hand witness and participant to those once or twice removed. I miss him, and his contagious excitement for the research process, but this paper gives a glimpse of that period.

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## PRACTICAL USE OF KONORSKI'S THEORIES

With modern knowledge of the mechanisms governing brain functioning, including the explosive increase in our knowledge in the field of molecular biology, concepts introduced by Konorski might be perceived as outdated. I strongly disagree with this view.

Zielinski's paper describes Konorski's theories and achievements in a thoughtful and elegant manner and also reflects greatly on the author himself. Both were deeply devoted to the field of conditioned reflexes and it was a pleasure and challenge learning theory and practice from them. I still vividly remember Zielinski's weekly group meetings – during which various aspects of Konorski's theories were analyzed in utmost detail. The challenge was to detect all potential weaknesses, while praising positive aspects, and to discuss all potential implications. His last paper is characteristic to Zielinski's fair, appreciative, while critical approach to the Konorski's work. I am deeply grateful to both of them for graciously sharing their knowledge with a graduate student and later brand new Ph.D. During these discussions I loved to disagree, not being particularly constrained by my lack of knowledge, and only now can I fully appreciate their patience. At the same time, I never thought that I would be using the theory and practice of conditioned reflexes in my work, as at that time my primary field of interest was electrophysiology. I could not be more wrong!

Konorski instilled in his students recognition of the enormous plasticity of the brain and strong belief that behavior may be explained and linked to processes within the brain. Reflexes were a tool in developing this understanding with modifications of the strength of functional connections and the principle of dynamic balance playing an important role. Nothing was stable forever, and Konorski's concept that extinction of reflexes is actually an active process, which changes the positive to negative correlation between conditioned stimulus and reinforcement has significant implication on mechanisms due to which learning, and particularly retraining occurs. The active role of formation of the inhibitory connections in the process of extinction had significant impact on the understanding of the brain functioning. Proposed by Konorski's in 1948 the mechanisms and rules controlling the modification of synaptic weights were later evident in Hebb's famous postulate (Hebb 1949) as well as in Albus' and Marr's theories of brain plasticity.

Theory and practice of conditioned reflexes became a crucial part of the neurophysiologic model of tinnitus and of Tinnitus Retraining Therapy, which is used to treat tinnitus and decreased sound tolerance (Jastreboff and Hazell 2004). Many of the puzzles of tinnitus can be explained only by invoking the theory of conditioned reflexes, including a number of Konorski's inventions. The concept of conditioned reflexes is expanded to encompass links between the sensory system and any system in the brain; consequently including the possibility of evoking any type of reactions, and not only motor reactions, as originally proposed. Nevertheless, the basic principles governing functional properties of these connections remain the same. Habituation (passive extinction) of tinnitus-evoked reactions is the goal of Tinnitus Retraining Therapy, with a process of habituation following some principles as proposed by Konorski. He pointed out the difference in detecting information and using/reacting to it. This is one of main concepts in modern theories of tinnitus, as the majority of tinnitus patients detect and perceive tinnitus, but do not react to it. Available data support the view that when reaction to tinnitus occurs, it reflects activation of the limbic and autonomic nervous systems coming from the auditory system, with development, sustaining, and potential extinction of this link governed by principles of conditioned reflexes. Moreover, a significant part of these functional connections occurs at the subconscious level.

Konorski's concept of classically conditioned fear plays a crucial role in the neurophysiological model of tinnitus and Tinnitus Retraining Therapy (Jastreboff 2004). Thousands of people around the world have benefited from the implementation of Konorski's concepts in that Therapy. Notably, after full appreciation of the role of reflexes in mechanisms of tinnitus and incorporating its consequences into clinical practice, the time needed to observe significant improvement in patients' condition decreased from 12–24 months to 3 months.

Konorski's work played an important role in directing our way of thinking about brain function, dependence of behavior from physiological processes in the brain, and mechanisms governing plasticity of the brain and specific aspects of learning and re-learning. His legacy remains important, and has a lasting impact on our understanding of brain function, even if his specific theories are no longer in the mainstream of current neuroscience.

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