

Looking back at Jerzy Konorski's book "Integrative Activity of the Brain", 45 years after

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This article presents historical background preceding writing and publication of Jerzy Konorski book "Integrative Activity of the Brain" followed by a short description of the main topics covered in the book. Two new and original contributions of Konorski are presented in detail, his theory of the motivational processes and the organization of the sensory systems in the brain. Those two contributions are then incorporated in the revised theory of the classical and type II conditioned reflexes which constitutes the core of the book. Conclusions point out at some of the ideas which remained valuable for the present day neuroscientists.

Key words: Jerzy Konorski, integrative activity of the brain, motivation theory, gnostic units, classical and instrumental conditioning, dynamic memory

INTRODUCTION

The monograph "Integrative Activity of the Brain" (IAB) was commissioned by a personal invitation to Professor Konorski issued in 1963 by University of Chicago Press. The book was finished three years later and published in 1967 (Konorski 1967). An expanded Polish edition was published by PWN (State Scientific Publishing House) in 1969 (Konorski 1969), followed by the Russian translation in 1970 by the "Mir" publishing house (Konorski 1970).

The book represents a bold attempt to summarize the then current state of knowledge of motivational and cognitive processes occurring in the mammalian brain. It proposed a whole new model of motivational and sensory processes in the brain, reviewed a large body of new experimental work on classical and instrumental conditioning, and presented new results on transient (dynamic) memory. Finally, it did propose a model of the integrative function of the brain.

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In this article, based on the presentation I gave at the Nencki Institute conference last September, I will describe the background of the book and Konorski's motivation for writing it. Then I will introduce the book and give a summary of the important and new ideas presented in it. Finally, I will try to confront some of the Konorski's ideas with the recent developments in brain sciences.

HOW "INTEGRATIVE ACTIVITY OF THE BRAIN" WAS RECEIVED

To some disappointment of the author, the book did not receive a worldwide attention. Indeed, only a handful of reviews of "Integrative Activity of the Brain" appeared in scientific journals following the publication (Konorski 1948, Andrew 1968, Gross 1968, Ochs 1968, Pampiglioni 1968, Williams 1968, Sołtysik 1970). One significant factor underlying the paucity of interest might have been rapid development of new methods in neurobiology which brought a wealth of new findings that would have been difficult to predict when the book was being written. Konorski was clearly aware of rapidly accumulating knowledge how the nervous system functions on the cellular level and

within specific neuronal systems. He called those new developments in brain science “an analytical approach”. This was clearly not his goal. Konorski’s main motivation to write the book was to present an overall picture how the brain works. He called this method “an integrative approach”. In fact, the title of his book was carefully chosen and it was a clear reference to an immensely influential book written by Charles Sherrington almost sixty years before: “The Integrative Action of the Nervous System”. Sherrington’s book summarized the state of knowledge about integrative activity of the spinal cord and motor centers in the brain.

The other possible factor for a lack of broad attention to Konorski’s book might have been quite common skepticism towards any grand theories in physiology. In fact, general physiology was at that time focused on specific functional systems and was little concerned with how the organism works as one entity. This was also true in brain research of the time. Another aspect worth mentioning might have been the fact that Konorski’s book was not an easy reading. It required a certain initial level of knowledge about the organization of nervous system and some familiarity with Pavlovian terminology. The Polish edition of the book two years later included a detailed glossary that helped the readers through the text which was at times dense with reported data, and with idiosyncratic terminology. Several years later Konorski admitted in his autobiography that the book probably had too much information, and probably should have been written as a two-volume set (Konorski 1974).

The book was certainly not very accessible for a novice in neuroscience. When it was published in 1967 I was one of only three PhD students at the Department of Neurophysiology of the Nencki Institute. I vividly recall the time when the newly published book was placed, with due reverence, on display at the institute’s library. The book seemed to have an invisible banner on the front page “For Adults Only”. Indeed, it took a quite long time before I could read and follow some parts of the book.

There are two admissions which Konorski made in the introduction to the English edition of the book which are worth mentioning. One comment referred to a well-known and influential article of the German etiologist von Holst thesis that, to quote Konorski, “*at the present stage of development of brain physiology the questions “how” and “why” are more important*

that of “where””. Konorski continues: “*In order to be consistent, when dealing with the problem of functional organization of particular system we shall make use of “block models” devoid of too precise anatomical specifications*” (IAB, p. 5). In other words, the localization of specific functions in the brain was less important than the understanding of their organization. I believe that such a strong statement will not be accepted by most of the neuroscientists today. The other Konorski’s admission follows immediately: “*if anyone should say that in this work we are dealing with the conceptual nervous system, we should readily accept this definition without considering it a reproof*” (IAB, p. 6).

BACKGROUND: KONORSKI’S BOOK AND HIS MOTIVATION TO PUBLISH

The previous book of Konorski which made him quite famous among the brain-and-behavior scientists was “*Conditioned Reflexes and Neuronal Organization*” (Konorski 1948). The book was published by Cambridge University Press in 1948. Konorski dedicated the book to I. Pavlov and C. Sherrington hoping that his work will help to bridge the gulf between their respective scientific achievements.

Within almost twenty years following the publication of his first book, a substantial body of new research had been accumulated by Konorski and his colleagues. However, most of this work was not widely known. It was published almost exclusively in the *Acta Biologiae Experimentalis* which was at that time the “house journal” of the Nencki Institute. The circulation of *Acta* in the 1950’s and early 1960’s was rather limited. The journal was distributed mainly *via* exchange with other scientific publications, institutions, and scientific libraries.

In 1955, Nencki Institute moved into a new building (in Luis Pasteur Street). The building was specially designed for biological research and had good facilities for the animals. The first few years were a period of intense activity at the Department of Neurophysiology. The Department consisted of several more or less independent research teams covering a wide range of neurobiological research. Political changes in Poland in 1955 made it possible for Konorski to travel abroad, broadened the Institute’s international presence, and brought there a number of visiting scientists from the West and East. In 1957 Professor Konorski was invited

for a longer visit in USA. There, to his pleasant surprise, Konorski found out that his monograph from 1948 was well-known and treasured by behavioral psychologists at several leading universities and research centers. This first visit allowed Konorski to establish scientific contacts with brain research institutions in USA and Canada. Shortly afterwards, Konorski renewed his scientific contacts in England (where he had spent some time just after WWII), and later with the brain research institutions in France and Italy. Of all those new scientific contacts, one American institution should be mentioned here. It was the Neurophysiology laboratory at the NIMH in Bethesda, led at that time by Dr. Eger Rosvold, an American of Norwegian descent. Dr. Rosvold's and his collaborators' research was focused on functions of the prefrontal cortex. A close cooperation was established between this laboratory and the Nencki Institute. Several important research projects were completed and published as the result of this collaboration.

Another place where Konorski had been always welcomed in USA was the laboratory of Professor Neal Miller at the Department of Psychology of Yale University. There, Konorski held a series of advanced lectures that had an important influence on several young experimental psychologists. Thus, in a short time Konorski became a well-known figure in American institutions. In 1963 Konorski was elected a foreign member of the National Academy of Sciences. At the time there were no other foreign members of the Academy from Poland. When in the early sixties financial resources for Polish science become available from the American Government, the Department of Neurophysiology of the Nencki Institute was one of the research institutions which received generous support.

The Polish edition of Konorski's book in 1969 had a new introduction which included extensive acknowledgments of Konorski's long-time collaborators and senior researchers at the Department of Neurophysiology. For unknown reasons, such detailed acknowledgments were missing in the English edition. The introduction to the Polish edition also contained some information that explained the general background and motivation for writing the book. Similar acknowledgments were given in Konorski's preface to the Russian edition a year later.

As mentioned before, by the early sixties, the Department of Neurophysiology consisted of several

research groups. Although all of the senior scientists in the department, with an exception of Professor Liliana Lublińska, had been Konorski's students and collaborators, they became quite independent in their research. Some of the senior staff members had been working for longer periods abroad; among them were Stefan Brutkowski, Hanna Chorożyna, Elżbieta Fonberg, Elżbieta Jankowska, Włodzimerz Kozak, Stefan Sołtysik, Remigiusz Tarnecki, Wanda Wyrwicka, Kazimierz Zieliński and Bogusław Żernicki. They all brought new expertise and new methods back to the department and developed their own line of research. Professor Konorski at that time, having many administrative duties, was involved directly only in some of the experimental work (with Genowefa Szwejkowska, Wacława Ławicka, Irena Stępień, or Czesława Dobrzecka).

There was no question, however, that he had a full overview of the research going in the Department. The Professor was very supportive to all new ideas and generously shared his own ideas. During his frequent trips abroad, Konorski was always presenting research going on at the Department and he would bring back some exciting news which he then shared with everybody at the nearest seminar. Very often, after a longer visit abroad, Konorski would come to the Institute directly from the airport, eager to hear what was happening during his absence and happy to tell "hot" news from his trip.

The other fact which should be mentioned here and which is relevant for some parts of the book is that Konorski maintained continuous interest in clinical studies of patients with localized brain damage. Over many years, Konorski had established a close contact with Department of Neurosurgery of Polish Academy of Sciences, led by Professor Lucjan Stępień. In collaboration with neurosurgeons and with the prominent neuropsychologist, Dr. Maruszewski who was a student of the Great Russian psychologist Alexander Luria, Konorski suggested new classification of aphasias. Konorski interest in neuropsychology was first aroused during WWII, when he worked for a short period of time at the military hospital in Tbilisi, Georgia, treating soldiers with a variety of brain wounds. Although Konorski completed medical studies in Warsaw that short hospital episode during WWII was probably the only time when he actually practiced medicine.

Konorski maintained broad contacts with Soviet scientists from the brain research institutes in Moscow, Leningrad and Tbilisi. Those connections were to a large degree based on personal familiarity with the leading Soviet neuroscientists. Other contacts were from the time Konorski worked at Pavlov's laboratory, and some from the period of his work in Soviet Union during WWII. Konorski was also one of the initiators and organizers of the collaborative meetings of the brain research institutes of the Soviet, Czechoslovak and Polish Academies of Sciences. All those broad international contacts gave Konorski quite a unique position among neuroscientists in Eastern European countries and in the so-called Soviet Republics. One can safely say that Konorski and his colleagues at the Nencki Institute established an important "brain science hub" where scientists from both East and West could share their findings and exchange ideas. In fact, the famous Wednesday seminars of the department were almost routinely carried on either in English or in Russian (once or twice even in French which was Konorski's favorite foreign language). Those bi-lingual seminars were due to the constant presence of guests from abroad.

NEW RESEARCH CONTRIBUTING TO THE PUBLICATION

Probably the most important argument for writing a new book was the fact that several new findings made by senior researchers at the department had direct implications for the theory of type II conditioned reflexes, a theory which was practically unchanged since early discoveries made by Konorski and Miller in the late twenties and described in a series of papers in early thirties (Miller and Konorski 1928).

Professor Wanda Wyrwicka, in a series of original studies of type II conditioned responses, had shown that in order to explain conditioning process it was necessary to include activity of the motivational center which participates in forming of associations between conditioned stimulus and motor response. When such association was established, activation of the motivational center by direct stimulation evoked the conditioned response. Lesions of the motivational center abolished existing responses or made it extremely difficult to establish new conditioning. In a series of studies, using goats as experimental animals, Wanda Wyrwicka was able to localize motivational centers

for hunger and thirst in the lateral hypothalamus. Another important finding came from work of Stefan Sołtysik. On the basis of his experiments, Sołtysik suggested that motivational center in the hypothalamus has two independent elements, one responsible for motivational drive (hunger center) and one responsible for consummatory response (satiety center). In his original experiments, Sołtysik was able to show that activation of the drive center is necessary for appearance of conditioned response, while activation of the consummatory center when the food reinforcement was available inhibited the activity of the hunger center and, as a consequence, reduced the motivational drive.

The next important discovery was made in the laboratory of Elżbieta Jankowska and Teresa Górska. They found that afferent input from the movement (dog's paw) was not necessary for acquiring and performing of the Type II conditioned response. These findings seriously challenged the original theory of Konorski and Miller which suggested that association between cortical centers for movement and the conditioned stimulus was the basis for acquiring type II conditioned responses. Further experiments conducted by Remigiusz Tarnecki had shown that evoking movement by direct stimulation of the motor cortex cannot transform this movement into a conditioned response, while stimulation of the sensory cortex may serve as a stimulus for conditioned response, again pointing out the kinesthetic feedback might not be essential for establishing type II conditioned responses.

In the light of those new results, it was clear that the explanation of the Type II instrumental conditioning needed a major revision. Likewise, new findings on the organization of motivational centers in the hypothalamus called for a revision of traditional view of the reward and punishment in classical and instrumental conditioning. At the same time, during early sixties, neurophysiology of the sensory systems had been developing rapidly. Experiments with recording of single neuron's activity in the somatosensory area of macaque monkeys initiated by Veron B. Mountcastle in and further developed by David H. Hubel and Torsten N. Wiesel in their studies of visual cortices of cats provided new insight about processing of information in the sensory neocortex. Professor Konorski keenly followed those new findings and during frequent exchange of ideas with Nencki's own visual physiologist, Włodzimierz Kozak, realized that the

emerging picture of the sensory systems had important implications for the general theory of learning and conditioning. On the basis of this new knowledge about the organization of the visual system and his longtime interest in perceptual deficits following localized brain lesions (different types of agnosias) Konorski formulated a new theory of functional organization of the sensory systems.

To sum up my introductory comments, it is clear that by the early sixties, research activity at the Department produced a substantial body of new results which required some kind of synthesis and incorporation into a bigger picture of how the brain works. Some of the new results directly challenged mechanisms previously postulated for establishment of classical and instrumental conditioned responses. Thus, we may finally state that the invitation from University of Chicago Press to write the book was very timely, and Konorski was ready for the task.

A BRIEF DESCRIPTION OF THE BOOK

“Integrative Activity of the Brain” consists of 13 chapters grouped into several main themes. The introductory chapter describes in detail the basic motivational activities of the brain. The next four chapters are devoted to sensory systems called, following a Pavlovian tradition, “the analyzers”. The first two chapters describe hierarchical and categorical organization of sensory systems and the following two chapters deal with the consequences of such organization for the associative properties of sensory systems. As mentioned before, the central concept of the proposed theory was idea of “gnostic units” as a high level of representation of sensory stimuli by a single neuron or a small network of neurons.

The next six chapters of the book are devoted to a detailed description of classical (Type I) and instrumental conditioned reflexes (Type II). Konorski made a major revision of the theory of classical and instrumental conditioning incorporating into his model a dual character of the motivational systems in the brain as well as his new theory of “gnostic units” and sensory associations.

The last two chapters of the book are devoted to the description of transient (dynamic) memory and to a recapitulation of the main points concerning the functional architecture of the brain and its integrative activity.

BASIC MOTIVATIONAL ACTIVITIES OF ORGANISMS

The introductory chapter of the book presents several new concepts related to basic activities of organisms and motivational centers in the brain. Following the Sheringtonian and Pavlovian tradition, Konorski defines activity of the nervous system in terms of reflexes.

Two general classes of reflexes are introduced: preservative reflexes which include all of the important tasks of the central nervous system (CNS) in maintaining normal function of the organism (called usually homeostatic functions) and protective reflexes that serve the function of activating organism to acquire desirable or necessary objects and to defend the organism against harmful stimuli and conditions. Within those two general classes of reflexes, Konorski distinguished the appetitive and defensive reflexes depending on the value of stimuli for the organism; the first class being directed towards acquiring of necessary or required stimuli and the second towards avoiding harmful or threatening stimuli.

The new and important distinction in motivational processes of the organism was built on the sequence of occurrence of specific activity. Konorski introduced two new concepts: preparatory and consummatory activity. The first form of activity consists of behaviors that provide organism with necessary incentives or allow avoid harmful and unpleasant stimuli. The second form of activity is a reflexive, unconditioned response of organism to the presence of the biologically important stimuli. This distinction will play a major role in a new theory of the classical and instrumental conditioning presented later in the book.

A result of such classification, Konorski defined a “quartet” of basic activities: preservative-preparatory and preservative-consummatory (appetitive) and protective-preparatory and protective-consummatory (defensive)

As an example of appetitive activity, Konorski described the organization model of hunger-satiation system; for the defensive activity he described the organization model of fear-relief system. Both models are represented by conceptual diagrams without a description of the brain centers (nuclei) and pathways involved. Based on the then latest studies on effects of electrical stimulation and lesions in the lateral and medial hypothalamus on food intake behavior of goats

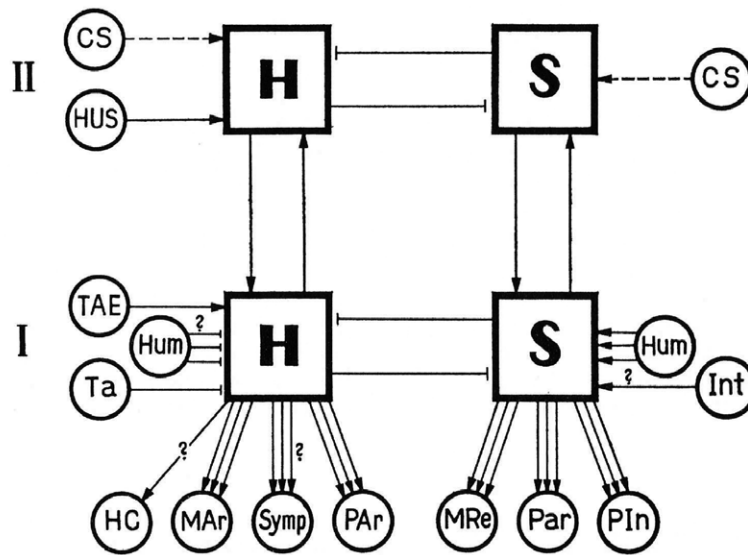


Fig. 1. Block model of the hunger-satiation system (simplified) (IAB, p. 28, © 1967 University of Chicago Press, by permission)

and rats, Konorski constructed a “block-diagram” of the hunger and satiation centers in the brain (see Fig. 1). The main points of this model were as follows:

Preservative alimentary activity is controlled by two subsystems, which will be called the hunger subsystem and the satiation subsystem. Each of those subsystems has a lower and a higher center.

The lower centers for hunger and satiation are localized respectively in the lateral and medial hypothalamus while the higher centers are represented in the limbic system (most likely in the amygdala where lesions of baso-lateral and medial nuclei produced opposite effects on food intake).

The lower centers of hunger and satiety are responsible for the consummatory responses, and their activity is controlled by a number of “hard-wired” (unconditioned) inputs such as taste stimuli, humoral substances, and interoceptive stimuli from the digestive organs.

The higher centers of hunger and satiety system are responsible for the preparatory-appetitive responses. At this level, conditional responses are being formed by association of the neutral stimuli with the presence of the unconditioned stimuli. Within hunger and satiety systems the lower and higher centers excite each other, while at the lower and higher levels hunger and satiety are mutually inhibitory.

Konorski pointed out that activity of the hunger center induces a general activation of motor responses and arousal in the sensory systems. Both responses

have a clear biological significance by increasing a chance of correct motor responses and enhanced alertness towards the relevant sensory stimuli. The essential point of the model is that the consummatory centers are “hard-wired” while the preparatory centers allow associations between the unconditioned and the neutral stimuli.

A similar two-level model was proposed for the “fear-relief” system. Fear was considered as a primary defensive response to pain stimuli while averting of pain activates a relief response. According to the model, both fear and relief are unconditional responses to nociceptive stimuli and they have a reciprocally antagonistic influence on each other. Activation of the fear center in the hypothalamus elicits a set of motor, sensory and autonomic responses, while activation of the relief center eliminates those responses (calming effect). According to the “block model” suggested by Konorski, the lower centers of “fear-relief” system were localized in the lateral hypothalamus (precise localization was not established) while higher centers of both fear and relief were localized in the amygdala and other parts of the limbic system. Similarly, as in the hunger-satiation model, the lower and higher centers of fear and relief are mutually excitatory while at each level fear and relief centers are mutually inhibitory.

Konorski briefly described two other forms of basic of protective preparatory activity: aggression/anger and exploratory behavior. Both forms of activity repre-

sent important motivational mechanisms for interaction of an organism with the environment. However, there was not enough information available about the localization of brain centers involved in these two forms of motivational activity.

In the summary of this first chapter, Konorski proposed a new definition of “drive” and, what he named “antidrive” as the behavioral expressions of all preparatory activities. Subjective experiences corresponding to particular drives were defined as emotions. What seems to be still relevant and important today is Konorski's attempt to define motivational activities of the organism in strictly physiological terms. The other important contribution was defining motivational systems in terms of antagonistic organization of the “drive” and “antidrive” centers. That is to say, that for each basic motivational state (a drive) there must be an antagonistic state or process (antidrive) that inhibits this drive and brings an organism back to equilibrium. Regrettably, the motivational process defined as “antidrive”, Konorski's ‘orphan’ concept, has not been adopted by modern neuroscience.

A number of important findings in the last decade have confirmed that, at least for hunger and satiation, there are separate modulators controlling activity of specific neuronal populations in the hypothalamus and selectively inducing the state of hunger or satiation – according to Konorski's motivational model, eliciting drive or antidrive. What is the nature of “antidrive” for fear, aggression and exploration, maternal and sexual behaviors and where could they be localized in the brain is still a question of debate.

SENSORY SYSTEMS IN THE BRAIN (ANALYZERS) AND ASSOCIATIONS BETWEEN THEM

The next four chapters are devoted to structure of the sensory systems and to the mechanisms of associations between them. Those four chapters present probably the most original and the boldest idea about general organization of the sensory systems in the human brain. As I mentioned before, based on new electrophysiological findings of Hubel and Wiesel about sequential and hierarchical organization of the visual cortex, Konorski applied those findings to other sensory systems and suggested a uniform structure for all sensory processes – the “analyzers” as he called them.

The core of his model is a separation of the “transit units” which are elements of hierarchical processing of sensory information from the “gnostic units” which represent biologically meaningful stimulus patterns (see Fig. 2). Sensory process is organized first by extraction of elementary modalities of the sensory stimulus by specific receptors, and then by processing through several levels of “transit units” up the highest cortical level.

Konorski makes a clear distinction between two types of “transit units”; those which contribute only to the transmission of information and those which in addition to transmission communicate information to other parts of the nervous system. He called the second type the “exit units”. Thus, at the highest cortical level, all units are “exit units” and the area where they are localized constitutes the “exit field”.

Here I would like to quote directly Konorski's great conceptual leap. “(...) *having to our disposal the recent data derived from Hubel and Wiesel's experiments, we can extrapolate their findings and explain the origin of perceptions according to the same principles which were found to operate in the lower levels of the afferent systems. In other words, we can assume that perceptions experienced in humans' and animals' lives are represented not by the assemblies of units but by single units in the highest levels of particular analyzers. We shall call these levels “gnostic areas” and the units responsible for particular perception “gnostic units”* (IAB, p. 75).

Konorski admitted that although there is no direct electrophysiological evidence that perceptions are represented by single units of the gnostic areas, he was firmly convinced that there is enough indirect evidence to postulate that such units indeed exist in the brain. The hypothesis that human perception is a unitary phenomenon was based on the argument that we perceive individual objects, places, animals, faces and so on as a single percept, and only with additional effort we can detect elements which comprise those perceptual items.

There are several important properties of the unitary perceptions that, according to Konorski, fully justify his theory that “gnostic units” represent single perceptual objects. Here are some of those properties: Immediateness – occurrence in a single act of attention (evoked by targeting response); Integrity – appearance as a unitary percept and not a sum of elements; Complementarity – similarity of the elements taking part in unitary perceptions; Amendment – resistance

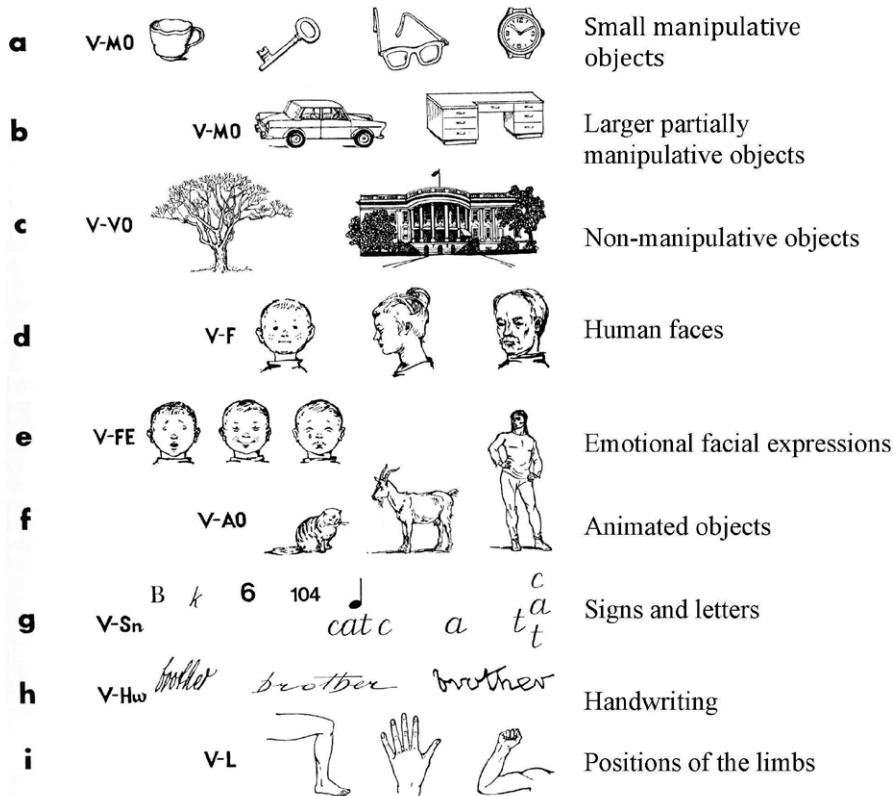


Fig. 2. Particular categories of visual stimulus-objects probably represented in different gnostic fields (IAB, p. 117, © 1967 University of Chicago Press, by permission)

to deformation of elements; Categorization – assembling single percepts in groups based on similarity.

In the next chapter, Konorski systematically described major categories of gnostic units in four sensory systems: vision, audition, somesthesia and kinesthesia. To identify primary perceptual categories, Konorski reviewed different types of information derived from physiological and psychological experiments, from the clinical symptoms in patients with sensory deficits, examples from the literature and his own introspective observations.

Konorski's description of the primary perceptual categories makes a fascinating reading. What is new and unique, in my opinion, is his categorization of the primary kinesthetic perceptions. Konorski pointed out that, in contrast to other sensory systems (analyzers), kinesthetic gnosis is based on stimuli produced internally by integrated patterns of movement. He defined such integrated movements as unitary behavioral acts and gave them general name of praxis. His analysis of primary kinesthetic perceptions revealed the following categories: skillful hand movements (hand praxis), patterns of body and legs movement (body praxis),

articulation movement of mouth (speech praxis) and locomotor movements in near space (space praxis).

The other unique trait in Konorski's analysis of gnostic units is a central position of language in all sensory systems. Konorski was very clear that language is a specific form of human behavior and that the perceptual aspects of language must have specific representation within all sensory systems. This postulate obviously implied hemispheric lateralization of gnostic categories involved in perception and generation of speech, writing and reading and thus leaving for the other cerebral hemisphere involvement in the non-verbal functions.

The final summary of all identified gnostic units in the sensory analyzers is presented as a block diagram named by Konorski "Conceptual map of the human cerebral cortex of the left hemisphere" (see Fig. 3). The map is a complex block diagram of the cortical surface with some adjacent structures. Localization of the boxes representing gnostic categories within each sensory system is only approximate, since Konorski made no attempt to correlate identified gnostic fields with Brodmann's cyto-architectonic map of the human cerebral cortex although the map

Conceptual map of the gnostic fields Brodmann's cytoarchitectonic map (1909)

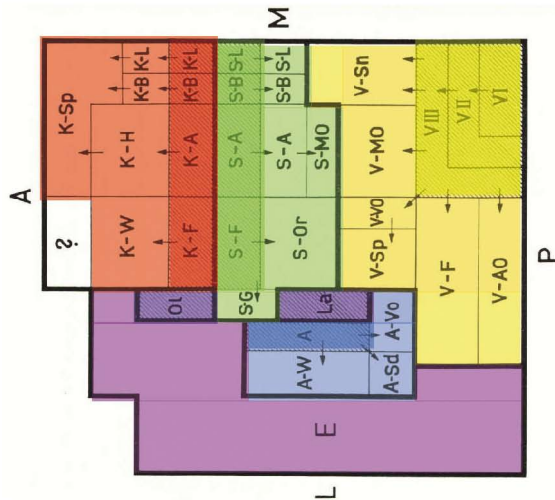


Fig. III-12. CONCEPTUAL MAP OF THE HUMAN CEREBRAL CORTEX OF

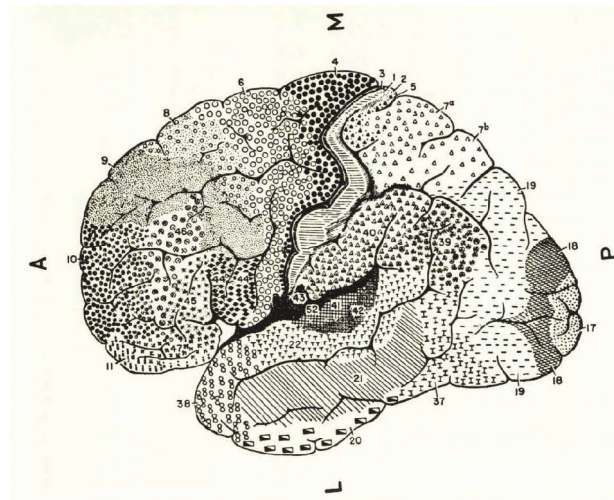


Fig. 3. Conceptual map of the human cerebral cortex of the left hemisphere (left) and the cytoarchitectonic map of that hemisphere according to Brodmann (right) (IAB, p. 160, © 1967 University of Chicago Press, by permission).

shown here on the right, was reproduced in the book along the “conceptual map”.

THE PROBLEM OF SENSORY ASSOCIATIONS

The next problem Konorski dealt with was how the sensory associations are formed in the brain. Having first described and justified the existence of gnostic units in the sensory areas, it was easy to argue that their main biological function is forming cross-modal associations and, more precisely, associations between the gnostic units from different sensory systems.

To illustrate the overall topography of sensory associations, Konorski presented five circular diagrams, again purely conceptual, without knowing if a particular connection has an anatomical substrate. Konorski divided all cross-sensory associations in the human brain into two major classes: non-verbal associations (many of them existing in animals) and verbal associations which are necessary for the understanding and production of language. Verbal associations were localized exclusively in the left hemisphere.

Chapter five of the book presents a detailed survey of associations in man and other mammals. Konorski systematically described all associations directed to each of the five sensory analyzers. There are many intriguing questions raised in the description of sensory systems and associations between them, and not to all of those questions Konorski had an answer. Some

of those open questions were how a specific sensory association is being formed in the brain, which associations are “pre-wired” based on exiting connections and which are acquired during the development and as the result of specific sensory experiences.

REEVALUATION OF CONDITIONING RESPONSES OF TYPE I AND II

The next six chapters represent the very core of the book. They deal with classical and instrumental conditioning. Here, Konorski systematically reviewed all of the major issues in theory of the classical conditioning, internal inhibition, the early model of instrumental (type II) conditioning and a revised model including the role of drive and antidrive in establishing alimentary and defensive instrumental responses. The major conclusion of the new model was that type II CR can be formed and elicited only on the basis of drive activation and preservation of response requires reduction or inhibition of drive after the instrumental response has been performed.

Following a detailed discussion of the new findings on the physiological mechanism of instrumental conditioning, Konorski presented the “Final version of the Block Model of Type II CR Arc”, shown in the figure below (see Fig. 4).

Here, Konorski introduced a concept of “central motor behavioral system” (CMBS) which includes all innate and acquired behavioral acts that the organism has at its disposal at a given period of life. There were

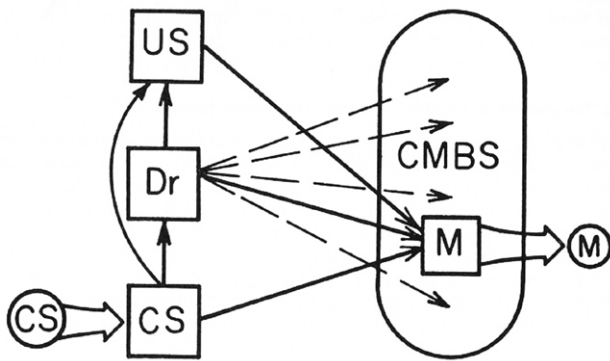


Fig. 4. Final version of the block model of the type II CR Arc (IAB, p. 447, © 1967 University of Chicago Press, by permission)

two major implications of this model; first that only those movements can be instrumentalized which are mediated by the central behavioral system, that is the movement performed by organism itself. The other implication was that a given motor act has unitary character and that no peripheral feedback is necessary for its instrumentalization.

The text of those six chapters is dense with information, with examples of individual experiments and references to the canonical issues of the classical and instrumental conditioning. Those six chapters, in my humble opinion, could have been a book in itself and one "for adults only". My recurrent thought during reading this part of the book was that all those sophisticated experiments of instrumental conditioning, brain lesions, direct brain stimulation and de-afferentations were dealing with animal models of quadrupeds, the animals in which extremities are primarily used for locomotion. Thus any instrumental movement of the extremities invariably involves a change in the position of the body, as well as other motor adjustments difficult to control in the experimental settings used for conditioning within each sensory system. What about primates and humans where the evolution created unlimited freedom of hand movements? What about the eye movements guided by visual attention? What about articulation movement necessary for generation of speech? Are they all dependent on motivational drive?

THE PROBLEM OF TRANSIENT MEMORY

Chapter twelve of the book deals with the complex subject of transient memory (called also dynamic or

recent memory). Konorski and his collaborators studied this problem for many years. They developed special tests to study transient memory in dogs and monkeys and made a significant contribution in search of brain structures involved in this form of memory. Regrettably, much of this work has been forgotten or misunderstood.

Unlike most of the memory researchers of his time, Konorski believed that processes of recent memory were not related to a temporary and labile phase preceding formation of stable memory, the consolidation process. For Konorski, transient memory had a function independent of the consolidation process, traces of transient memory need not to be consolidated and they appear and disappear depending on behavioral demands. Konorski's analysis of transient memory starts with analysis of its role in perceptual processes. Some sensory experiences and stimulus patterns have a transient character, they are not consolidated, and they are perceived only when paid attention to. Other stimulus patterns which are close to or belong to category of existing gnostic units, would form stable representations and could be evoked within a certain period of time. For Konorski, this was the most important property of recent memory in perceptual processes, meaning that some sensory patterns can reappear exactly the same way as new objects.

Konorski writes "*transient memory is not a privilege of only new objects (being said to serve for their consolidation), but it is a normal process following each perception*" (IAB, p. 494). Konorski made a clear distinction between the prospective and retrospective function of the transient memory. The first function provides sequence of images of future tasks that direct behavior to effective performance while the second function ensures remembering of the already completed actions. Malfunction of either form of transient memory results in disorganized behavior.

As far as the neuronal mechanisms of transient memory were concerned, Konorski firmly believed that this form of memory is based on a continuous activity in the "reverberatory circuits" of the cortico-thalamic loop. This opinion was mainly based on the experimental evidence from studies on the effect of electroconvulsive shocks and short anoxia episodes applied in different memory tasks. Regrettably, our knowledge in this matter has not advanced much in the last 45 years.

CONCLUSIONS

To summarize this short description of the book I would try to point out some of the central ideas developed by Konorski which, in my opinion, have not lost their importance or relevance.

First, Konorski's theory of the motivation as reciprocally antagonistic processes. The main point of the theory was that there are two opposite physiological functions that ensure motivational equilibrium, drive and antdrive. Both functions consist of dynamically regulated innate ('hard-wired') and acquired processes and are represented by the consummatory and appetitive responses. Without knowing what is the mechanism controlling the level of fear, aggression, sexual drive or drug addiction, we still adhere to the old thinking in physiology that is encapsulated in the saying "what is going up has to go down". Present day neuroscientists should take a closer look at Konorski's ideas of motivational processes.

Secondly, Konorski's theory of the gnostic units and organization of the sensory systems has been known only to a handful of sensory physiologists. In modern cognitive terms, what he called gnostic units would be called "representational processes". According to Konorski, gnostic units provide a neural substrate of sensory objects and allow forming cross-modal sensory associations. Gnostic units as envisioned by Konorski enhance memory capability and provide essential operational elements both for the transient and the permanent memory.

Thirdly, Konorski understood that language is the ultimate form of mental representations. For Konorski, language was the highest form of sensory and cognitive processes and the same time a complex form of behavior. However, in spite of Konorski's profound knowledge of clinical neuropsychology which gave him many insights into the organization and function of language in the human brain, in his book he did not provide a conceptual, neurobiological model of the language.

It is difficult to speculate why Konorski's book and his ideas have been overlooked for many years and are still not widely known. Perhaps it was the conceptual character of his theories how the brain works. For a long time, the rigorous study of behavior has not been valued by neuroscientists, and it was continued only by experimental psychologists for most of whom Konorski's book was probably too difficult. Perhaps it was Konorski's attitude to anatomical data that contributed to general skepticism.

By the time the book was completed and in the few following years, significant progress had been made with new anatomical techniques and in localization of specific functions in the brain. Finally, I would like to conclude this essay with a philosophical thought which seems irresistible to me, after revisiting the book and the scientific life of Jerzy Konorski. Great achievements in science come only with a passionate commitment and a great power of thinking. Konorski had both.

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