Neurons and neuronal networks (summaries of papers)

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Neurons and Neuronal Networks

(Summaries of Papers)

A one day meeting on this subject has been held at Prague on May 3rd 1967, organized by the Czechoslovak Cybernetic Society and prepared by a commitee: T. Radil - Weiss (Head), P. Nádvorník, Z. Wünsch.

Summaries of the papers presented follow.

Research Activities Related to Neurons and Neuronal Networks. (Introductory Remarks)

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Two different aspects of this research (a) the *biological* and (b) *the mathematical and technical* may be differentiated.

(1) A short description of the main histological, biophysical, neuro and electrophysiological results contributing to the contemporary *biological concepts* on neurons and neuronal networks was given. Most important are information directly related to the structure and function of neurons and networks. Although the activity of nerve cells and their aglomerations are the basis of the complex functions of the whole nervous system, synthetic study of its behavior realized on the basis of black — box approaches does not bring any new information on the specific laws governing the function of neuronal networks and may merely describe some aspects of the logic of action performed by the system. Therefore biological results as well as modeling related to complex phenomena like conditioned reflexes, learning, memory etc. does not contribute too much to our knowledge on neurons and neuronal networks.

(2) Modeling is the most important concept related to the *mathematical and technical aspects* of the matter. Positive heuristic role is the atribute of any true modeling. The projection of this heuristic function may be directed toward different fields. There cases may be differentiated. (a) *Biological models* have to improve our understanding of the biological substrate studied. The correspondence of these models to all biological data available and the close mutual interrelationships of the modeling with experimentation on the biological object is a common rule in this case. (b) *Theoretical models* and modeling of neurons and neuronal networks develop autonomically even they are triggered by some biological fatcs. Their heuristic significance lies in the field of mathematics itself and the

criteria for evaluation of these models is solved within the mathematical theory. No obligatory similarity exists with respect to actual biological results and concepts. (c) The aim of *technical or bionical models* is to bring something new in these branches. Their heuristic value is directed toward technical praxis and neither similarity to the biological substrate nor the exactness and purity of the mathematical formulation is a basic factor.

In the papers following just examples of different aspects related to the actual research activities of some of the Czechoslovakian laboratories will be given.

Some Techniques and Computer Programs for Analyzing of the Impulse Activity of Single Neurons

J. Škvařil, I. Krekule, T. Radil-Weiss, J. Syka, J. Valášek, P. Bureš, J. Vlach, *Laboratory of Neurocybernetics, Institute of Physiology, Acad. Sci., Prague and Computing Laboratory of the Technical University and. Czech. Acad. Sci., Prague.*

We define the impulse activity of single neurons as the realisation of a stationary and ergodic stochastic point process.

For evaluation of the parameters of this process we use mainly the two following methods in our laboratory:

1. The "on — line" analysis is performed by a modified pulse height analyser (type NK 103). The modification includes mainly the possibility of external control of the adress register. The pulses entering the register come from the external clock generator and not from the analog — digital converter of the analyser.

2. The "off — line" method includes a system for recording the impulse activity of a single neuron on magnetic tape. The general — purpose digital computer URAL 2 of the Computing Laboratory of the Technical University and Czechoslovak Academy of Sciences is used for performing the analysis. The conversion of intervals between consecutive spikes into numbers was performed by an electronically controlled key which controls the transition from the cyclic subroutine for time measuring to an other subroutine which records the time value in the memory. Beside that a system was built converting the data from the magnetic tape to a specially coded punched tape, which may be introduced into any computer directly.

We use the following programs for the evaluation of impulse activity of single neurons: Conversion of intervals from magnetic to punched tape; evaluation of estimators of the mean interval, standard deviation, coefficient of assymetry and coefficient of excess; scaled interval histogram with graphical output; poststimulation histogram with graphical output; evaluation of estimator of correlation coefficient of two consecutive intervals; χ^2 test of the hypothesis that the given impulse activity is realisation of a Poisson process; χ^2 test of normality of the intervals; Kolmogorov — Smirnov goodness — of — fit test for two empirical distributions; histogram of the first — order forward reccurence time intervals (this histogram is useful for testing the dependency of two stochastic point processes).

Spontaneous Impulse Activity in Some Regions of the Brain

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In rats immobilized by curare and fixed in a stereotaxic instrument the spontaneous impulse activity of 250 neurons has been recorded by extracellular glass microelectrodes. Samples lasting at least 5 min were recorded on magnetic tape and processed by the URAL 2 computer using the techniques described in the previous paper (Škvařil et al. 1967). The mean inter-impulse interval length, variance and coefficient of variation has been computed, and inter-impulse interval histograms constructed and plotted by the computer. Average values of these parameters (witn S. E. of the mean) and the incidence of different shapes of histograms has been expressed for groups of 50 neurons approximately in each of the experimental situations.

We have found that in unanaesthetized curarized animals the average values of the mean interimpulse intervals are: 135 ± 28 msec for the thalamic, 334 ± 89 msec for the reticular and 305 ± 43 msec for the caudate neurons. This value is significantly shorter (the frequency higher) in thalamic neurons in comparison with the two other structures. The average values of the variance of the inter-impulse intervals resembles the values of the mean interval length. As the shape of interpulse intervals histograms is concerned: the majority of neurons (93% thalamic, 53% reticular, 68% of caudate) shows a distribution close to exponential, the activity of many reticular neurons (33%) is fairly regular showing an interval distribution resembling that of Gaussian type.

By the anaesthetic dose of barbiturate the statistical parameters described above did not change considerably in this structure with the exception of an increase of the amount of neurons showing a bimodal distribution, despite of the deep influence of this drug on the physiologic function of the reticular formation.

The use of other types of statistical processing and the usefulness of an interdisciplinary approach to the research on neuronal networks combining (a) quantitative statistical histology, (b) the recording of the impulse activity from 2 or more neurons of a known distance between them and computer analysis of the time relationships of their activity with (c) modeling of some features of the networks, is discussed.

Some Problems of the Research on the Plasticity of Neural Networks

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Different approaches to conditioning at the single neuron level are discussed. The nonspecific unit activity changes acompanying gross behavioral conditioning cannot be used to identify the locus of the primary modification of the nerve net. A more straightforward approach is the direct examination of Hebb's (1949) assumption that new connections are formed between simultaneously activated neurons. When local stimulation of the recorded nerve cell is used as the unconditioned stimulus (US) or conditioned stimulus (CS), the number of interacting elements is considerably limited; this makes it possible to locate the plastic change more reliably Three modifications of the procedure are described. a) Gross CS reinforced by single cell US. b) Single cell US reinforced by gross US. c) Stimulation of one neuron (CS) reinforced by stimulation of another neuron (US) in the same areas. In an attempt to verify the first possibility experimentally an indifferent acoustic CS (2000/sec 0·9—3·0 sec duration) was reinforced by polarization of the recorded neuron through the capillary microelectrode (10—50 nA, 0·3—1·0 sec). A simple computer was used for both programming the experiment and plotting the results in the form of post-stimulation histograms. Although up to several hundreds of reinforcements were applied stable reactions to sound could be established only in 17 out of 128 neurons of the reticular formation, non-specific thalamus, hippocampus and neocortex of unanesthetized curarized rats. The low incidence of positive results may be due to a lack of auditory inputs in most of the examined neurons. Similar reinforcing procedure induced clear cut modifications of the original acoustic response in the majority of units displaying acoustic reactions from the onset. Mechanisms of the plastic reactions is discussed and its similarity with dominant focus, reflex sensitisation and heterosynaptic facilitation is stressed.

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Intracellular Activity of Subsequently Marked Cortical Neurons

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The method of marking single spinal motoneurons by staining with intracellular recording microcapillaries (Thomas and Wilson, Science 151; 1538, 1966) was modified for cortical neurons which are smaller and less firmly anchorded in the tissue than motoneurons. The recording microelectrodes were filled with 1 Mol. potassium acetate saturated with methyl blue. Immediately following the intracellular recording the pigment was introduced into the cell by electrophoresis (1 μA, 3 min., capillary negative). After fixation in formol and gelatine inbedding the marked cell was searched for in cryostat slices additionally stained with neutral red.

Some results are demonstrated presenting slides of unit activity records with the pertinent microphotographs of stained single neurons, from the somatesensory cortical area of rats under barbiturate anaesthesia. Besides pictures and intracellular records of large pyramidal cells stained often with processes and located at deeper layers, small round or stellate ganglion cells were found at the depth of 0·2 mm or also over 1 mm, well stained. Their intracellular records showed spontaneous activity of different character, which could be maintained over one hour, which was abolished by local penicillin (convulsive drug) application and which stopped for short intervals after elicitation of primary cortical responses to sciatic nerve stimulation. According to these characteristics the small neurons are identified as intracortical inhibitory interneurons.

In conclusion, we have succeeded to mark — by staining with the intracellular recording microelectrode — single cortical neurons from which intracellular unit activity recording had been accomplished, and this was the case not only for large pyramidal cells but also for small inhibitory cortical interneurons whose accessibility to intracellular recording has been questioned till now.

Mathematical Modeling of the Spontaneous Impulse Activity of Neurons

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These models may be divided in two characteristic groups. (Moore et al. 1966).

The basic assumptions applied in the first group (i.e. Stein and others 1965) are the following: Excitatory and inhibitory impulses occur randomly with a mean frequency f_e and f_i, respectively; after each firing there is a refractory period of duration t_c; at times $t > t_c$ an excitatory impulse produces n units repolarisation; if the depolarisation reaches a threshold of r units, the neuron fires; for subthreshold levels, the depolarisation decays exponentially between impulses with atime constant τ.

A general expression for the distribution of neuronal firing intervals for this model is not known and the author had to rely mainly on the results of Monte Carlo simultions.

In the second group of models (i.e. Geisler and Goldberg 1966) it is assumed that the membrane potential is a random voltage $N(t)$ with a Gaussian amplitude distribution. Whenever the membrane potential exceeds the treshold voltage (which is constant or decays exponentially), the neuron discharges. It is assumed that the random noise $N(t)$ following a discharge is uncorrelated with the random noise that preceded the occurence of that discharge.

It is evident that there is intimate connection between these two groups. It is a question however whether it is possible to approximate the subthreshold changes of membrane potential in all cases by Gaussian process.

Our neuronal model is similar to the model of the first group except that it assumes a great number of inputs to be present; at each input trains of impulses occur which we define as a stationary and ordinary stochastic point process. The instants of changes of the subthreshold membrane potential are thus given by superposition of a great number of stationary and ordinary point processes. In limit this superposition approaches the Poisson process (Chinčin 1955).

It is clear that the output pulse may be generated only when some input pulses occur. Then the distribution of output intervals is defined by the distribution of sum

$$Z_n = \sum_{i=1}^{n} z_i ,$$

where $Z_1, Z_2, Z_3, \ldots$ is a sequence of independent random variables with the same negative exponential distribution with mean value λ and n is a random variable taking values $1, 2, 3, \ldots$ with probabilities $P_1, P_2, P_3, \ldots$ The expected value of this sum is (Wald 1944)

$$E(Z_n) = \lambda \, E(n)$$

and other moments are also known.

The problem of finding the distribution of output intervals is then reduced to the evaluation of the distribution of n. One approach to this problem will be discussed in another paper.

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Some Aspects of Modeling Neuronal Networks

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On the basis of histological data on the density of neurons in some structures of the brain a hypothetical neuronal net has been conceptualised and an electronical model realised, which has to be used for modeling some brain structures and their spontaneous impulse activity.

We consider the type of axo-dendritic arborization. The following values on structure are considered (Young J. Z.: A Model of the Brain, Oxford 1964, Lauria F. E.: Journ. Theor. Biology, 1965, 8): density of neurons $\nu = 4 \,.\, 10^4/\text{mm}^3$, number of synapses on the dendritic tree of one neuron $\xi = 2 \,.\, 10^3$. The average value of synapses between the dendritic and axonal trees of two different spacially overlapping neurons has been estimated. The number of synapses of this type is

$$S = \frac{S_a}{N_d} = 1{\cdot}55 \quad (\text{for } R_a > R_d)$$

where S_a is the number of presynaptic endings on axonal tree of a cell within the space of the dendritic tree of an other cell; N_d is a number of all the neurons occuring within the space of the dendritic tree.

Considering neurons oriented in any of the possible directions in space, much lower probability of functional connections has to be supposed.

Some Properties of Synaptic Memory

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Author's model of synaptic memory is based on a three-layer neuronal net, consisting of input elements S_i, associative elements R_j and output elements R_k. Each S_i is connected to all associative elements whose outputs a_j are equal to s_i being the amplitude of the signal from S_i and u_{ji} the respective synaptic weight. The set of a_j values at a given time represents the "diffuse transform" of the input pattern by which it is evoked. The changes of the synaptic weights u_{ji} resulting from "learning" are brought about autonomously in separate neurons as a function of the respective input and output signal, s_i and a_j, without any central controlling element. Under rather general conditions repeated simultaneous occurence of two elementary stimuli leads to positive correlation between their diffuse transforms.

The changes concerning associative synaptic weights can be studied by means of a special type of output, the "backward transform"; a neuronal net provided with it operates like a retranslation system reproducing the input pattern; it can be shown that a growing organization of the net originating from "learning" causes the backward transform to differ from the original pattern, behaving as a source of distortion.

Two interesting phenomena are described: "mediated" correlation appears between transforms of stimuli which had never occured simultaneously, by means of another stimulus correlated to both of them, which enables to explain the origin of complex reflexes; then there is the process of "forgetting", i.e. weakening correlation between transforms of stimuli which do not occur simultaneously any more but enter other input combinations. This process is especially interesting from the quantitative point of view: it appears that the residual amount of correlation cannot sink below a certain level.

It is also shown that as a result of space perception topological relations originate in the space of diffuse transforms and eventual backward transforms; thus we can illustrate that such relations can only arise after relatively long periods of learning.

As to the perspective of further work: it will be advatageous to extend this model by including the reverberation (short-term) memory, thus enabling to deal with a broader group of psychical phenomena, especially to explaing the principles of time sequences coding.

The Neuronal Net as a Regulated Structure

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If we hold the whole nervous system for a neuronal net, then the elements of this net are differenciated and so are the relations between them. As the structure of the net we denominate the differenciation and the way of arranging of the neurons in the net.

The question of the relation between the structure and the function of the net is connected to some problems, i.e. the problems of functional abilities (the problem of the CNS as a very complicated black-box) or the problems of analysing the possibilities of disorders in the CNS. Related is the problem of specification of the relevant aspects of the structure of a net with regard to the functional abilities of this net.

The process creating the neuronal net (construction by evolution and development) is one of the factors determinating the possibilities of the functional abilities of the resultant net and the relations between the structure and the function also. We do not suppose the construction process realizing an a priori plan of structure or of functional abilities. Indubitable, however, the result is a product of a process having a goal-directed character which makes possible the evolutionary improving of functional abilities of the net. This improving is effectuated by changing the structure.

The method of construction of the net may be conceived as a system having two distinguishable functional constituents: the process generating the structure and the control of the generating process. Known biological facts may form the basis for modelling some aspects of the considered system. Stimulations to such experimental models may be found in the papers of von Neuman, Barricelli and others.

As far as the direction of the goal-directed process is concerned, on the basis of a possible interpretation of some facts the changes may be simplified expressed by two symptoms: 1. the possibility of creating more complicated automata, 2. the growing possibility of realizing different automata in a given net and of selecting between them.

Consequently the growing ability to simulate different automata may be the way to optimisate the functional possibilities of the net. Let us assume, that the form to operate these simulated automata is a process analogous to the considered system generating and cotroling the structure. The prerequisite for this possibility may be the rise of a structure of the net having some features of the universal embeding spaces for automata (in the sense of Holland, Moor). With regards to this hypothesis it is possible to formulate one of the general problems of regulation of the structure of neural nets.

Some Mathematical Models of the Higher Nervous System Activity

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Although the higher nervous activity includes a complex of a large number of single psychophysiological mechanisms, as for instance memory, recognition processes and the like, it may be described in general comparatively simply as behaviour. Let us assume the behaviour to be a reaction to the given situation or rather the choice of a decision in the given situation. The formulation seems to be a suitable one giving on the one hand basic features of the normal psyche of every individual and on the other implying an analysis of behaviour and of elementary similarities.

Two methods are employed by the present authors in the mathematical study of the behaviour defined in such a manner. In the first case the authors assume that the endings of the corresponding receptors are topologically near. The model works on the basis of generalization of the se called weight model where not only the weights of the individual signs, but also the weights of pairs and groups of n-members are of consequence. Strengthening of these weights with a favourable result in general behaviour and weakening with an unfavourable one are assumed. In the second case the geometrical distance plays no role.

It is assumed that a system of situations S is given. A system of behaviour of decisions $R(s)$ and the functional $F(R(s))$ are applied to every situation. The aim of the activity of the organism is to reach the most favourable values in every situation, i.e. the highest values of this functional. Finite countable or uncountable sets of situations as well as finite countable or uncountable sets of decisions in every situation are considered.

The authors have described general conditions of forming the algorithm how to find the system of decisions convergent to the optimum decision.

Present Neurophysiological Conceptions on the Activity of CNS and the Possibilities of its Modelling

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A new approach to the research into the acticity of the central nervous system is the employment of cybernetic methods attempting at formation of a hypothesis on CNS structure by gathering the knowledge gained in the physiology of behaviour and the physiology of CNS and trying to examine it by modelling. The large number of data which are at our disposal at present cannot be fully used for making general hypothesis on CNS structure because of their lack of order and arrangement. Therefore simplified assumptions may be employed only. The correct classification of the initial assumptions is of basic importance for the value of the hypothesis made.

From the results of physiological investigations of CNS we have tried to select those which make it possible to create a uniting hypothesis on the fundamentals of CNS activity, the knowledge of its phylogenetic development being considered the most important aspect. The essentials of the hypothesis lie in the model of transmission properties of the universal element based on the verified experience with the properties of neuron and broadens them by the ability of developing lasting structural changes. The element with these properties could constitute a building stone of a network providing at any moment the possibility of any temporal or lasting change in its behaviour called forth by the acting stimuli only.

An electronic model of the element has been designed, on which the basic properties of the assumed structure were tested. The main criterion of suitability of the hypothesis will be an attempt at modelling with these elements of a more complex network and a confrontation of their properties with the results of physiological tests. Basic experiments with modelling the network on an analoque and automatic computer have already shown some interesting analogies.

The "Pseudouniversal" Automaton as an Element in Adaptive Logical Nets

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A device is described briefly, capable of simulating a relatively large group of automata, given that the nomber of their states does not eccees a fixed value. The device simulates the behavior of a person, knowing how to read a representation of a finite automaton (e.g. its canonic table) and instructed to find out the future inner state of this automation and its output state, according to the input words and an initial inner state told to him. Obviously, such a person simulates by his behavior the behavior of the automaton the representation of which he reads. The "instruction" told to that person can be realized by a special type of finite automaton. The realization of such an automaton can be performed in various ways. One of these is reported, consisting of a device in the form of a logical net with a reading head, capable to read binary coded tables of finite automata. The equations of this net have the following general form:

$$q_j^{t+1} = \bigvee_{i=1}^{2^n} [\mathop{\&}_{j=1}^{n} (x_j^t \equiv \xi_{ij}^t) \& \eta_{ij}^t] ;$$

$$z_j^t = \bigvee_{i=1}^{2^n} [\mathop{\&}_{j=1}^{n} (x_j^t \equiv \xi_{ij}^t) \& \zeta_{ij}^t] .$$

After considering some properties of this device, beeing a concrete model of a larger class of "pseudouniversal automata", some properties of nets formed from such elements are breifly mentioned. It is shown, that thay exhibit a considerable plasticity of behavior.

The hypothesis is discussed that there may be nervous systems whose elements are such "pseudouniversal automata" in the view of recent theories about non- neural forms of memory storage.

The Problem of Artificial Intelligence from the Viewpoint of Neurophysiology

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The problem of artificial intelligence is usually approached by modelling the mechanisms of human thinking.

In a model of their own, which was programmed for an automatic computer, the present authors made the following assumptions:

1. In agreement with Sečenov-Pavlov's theory, thinking may be considered as conditionally reflexive activity, in which, besides real (first signal) stimuli, word stimuli are primarily employed. These concept (second signal) stimuli are deposited in memory. The memory as a model of relations of the individual

to the surroundings offers in this manner inner "virtual" stimuli for the choice of variants of behaviour.

2. An association principle has a place in thinking. Attaching of concepts to logical operations is governed by the value of probability relations between the concepts.

3. The word is the concentrated element and the general means of modelling in the region of the psyche.

The programme for the computer was prepared in such a manner that after introducing small children's vocabulary into the memory of the computer, weight relations between pair words were formed by repeating. Then the computer was able to select and chain the concepts which belong to one another logically. The computer even attached new words by being given an information which concept category the new word belonged to.

Some Results of Training of an Adaptive Threshold Element

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This information presents some results of training of an adaptive threshold element. This element can specifically react to new information on the basis of past experience. This experience is obtained during a training procedure from a teacher. This teacher feeds simple patterns to the machine and shows the desired output. During the training the variable weights are automatically adjusted for the machine to react as desired. After the training phase this machine can classify input patterns in a moment acquired during the training phase. The model of an adaptive threshold element was realised and applied to some experiments in adaptive EKG diagnosis. An experiment done in cooperation with Doc. Šilink, Dr. Sc. has showed the ability of diagnosis in clinical medicine. The probability of correct responses was between 83% and 100% and depended on the choice of codes applied to symptomatologie and on the number of trained samples. The second experiment was made with a simple neural net and multi-bit input patterns. Input patterns were coded by spoken words. A series of experiments was performed to determine how well the adaptive system can recognize two sets of words or different speakers. The designed net has operated quite well and the used coding has been suitable for the recognitions words and speakers.

Adaptive Learning Control Systems

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In this information some applications of models of one neuron or neural nets in Automatic Control are presented. The adaptive learning system modifies its control parameters to improve its performance as a result of its experience under unpredictable changes of environment. As the adaptive learning controller an adaptive threshold element called adaptive linear neuron (ADALINE) is used. The state of a plant is described at any instant by the values of its state variables. These variables are coded and presented as input patterns of one neuron. Neuron output acts as a bang-bang control. A realised neuron of this type was used as a minimum time optimum controller and as a controller maintaining the system in the desirable state.

In many problems in automatic control more than two level controllers are necessary. This is realised by a neural net of parallel neurons. For selflearning feedback loops are used. Some aspects of selflearning are already realized at one neuron.

The aim of learning is given by an index of performance, mostly in an integral form. The extremum seeking devices changes the parameters of the controller as the index of performance will be decreased bellow a certain value. A selflearning system can be used for modelling both structure and parameters of controller to certain plant. Plant characteristics identification is another application of learning systems.

The Neuronal Model as a Functional Unit for Automation

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Neuronal models based on the modulator — demodulator concept may be used in principle for building automata.

A functional unit of this type combines some of the advantages of analog and digital techniques. It is not directly coupled but it has an analoge output (expressed as frequency).

The following mathematical operation could be performed using networks of these unis:t

1. Algebraic addition and subtraction;
2. generation of functional relationships;
3. integration;
4. logical operations.

Using memistors as memory units, networks may be constructed capable to change their function on the basis of information from the system regulated.

As an example we show a network acting as a function generator, which may be adjusted by changing the value of threshold h and the weight of interrelationships for any type of function $y = f(x)$.

Application of the Neuron Networks Theory to the Description of Automatic Industrial Equipment

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The description of behaviour of automatic industrial equipment (in particular time intervals, with a number of binary output and input parameters) by means of time and motion studies, logic matrices and schemes is inadequate, especially in cases of asynchronous automatic equipment equipped with internal memory. In these cases the transcription of logic schemes into equivalent neuron networks is recommended enabling the deduction of all possibilities of behaviour of the automatic equipment.

As an example a detailed description of behaviour of a logical gate of the adaptive control system of selecting and holding the optimum load of mining and ripping machines, is given.

By means of the given method the description of behaviour of packaged units of the automatic signalling in mine road junctions, is worked out. After the particular packaged units of the control system of integrated data recording, transmission and processing for purpose of operational deep mines process control have been designed, the correct function of particular elements and complete assemblies will be checked by means of the given method.

Neurony a neuronové obvody

Jednodenní seminář na toto téma uspořádala v Praze dne 3. května 1967 Čs. kybernetická společnost. Jsou uvedeny výtahy přednesených příspěvků.