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AN ATTEMPT AT MODELLING OF THE CENTRAL ALIMENTARY SYSTEM IN HIGHER ANIMALS

III. SOME THEORETICAL PROBLEMS CONCERNING IDENTIFICATION AND MODELLING OF THE SIMPLE NEURAL STRUCTURES

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INTRODUCTION

There exist two approaches to the problem of modelling of processes in physical, technical and biological systems. They differ both in general aims and in methods. The aim of the first approach is to design and construct (or to program on a digital computer) such an arrangement which simulates fairly well the output of the processes in the modelled system, when input values are known or given. In this approach we are not interested in whether the internal structure of the model is similar to the structure of the modelled system. The only condition is that the structure of the model should be as simple as possible. Such approach is known as a "black box" method, and is often used when, firstly, we have a very meagre information about the internal structure of the modelled system, and secondly, we are interested only in simulation of the processes on the outputs, and not in identification of structure of the investigated system. Such a situation occurs also in some systems of automatic control. In that approach the procedure consists in determining the correlation between output and input processes, that is, between reactions and stimulations. In many cases statistical methods are useful, and especially factor and regression analyses.

The second approach is more interesting for us. Its aim is to establish as exactly as possible the internal structure of the modelled object.

It must be stressed that even the most extensive and precise investigation of the output and input processes does not give the possibility of unequivocal determination of the internal structure of the biological or technical system, except in very simple and elementary cases. In order to determine the internal structure we must have as much preliminary information as possible about the processes and principles of functioning of those parts of the system to which we do not have direct access through inputs and outputs.

In neural structures, as well as in some technical arrangements, such information consists in determining the properties of their elements, and in particular of general principles of the functioning of these elements. In the case of the nervous system the problem consists in determining the principles of transmission and transformation of stimuli in the nerve cell, or speaking more technically, in the data processing principles in the neuron. The properties of the elements used in our model of the alimentary system correspond to our knowledge about data processing in nerve cells, and were described in the previous paper of this series (Gawroński and Konorski 1970). In short, they may be described as summing elements with threshold characteristics and saturation.

Further information about the modelled system concerns the connections between its elements, that is the structure of the system. Only in exceptional cases do we have enough information about this structure. In such cases modelling consists in setting up such parameters of the elements and connections as to get satisfactory correspondence of the results of modelling with physiological or physical experiments.

Because of the lack, in the present stage, of exact mathematical methods enabling the determination of the unknown internal structure we must usually take into account the two following kinds of information.

1. The direct information which we get from anatomical and physiological investigations (the effects of lesions, direct stimulation of centers and so on).

2. Indirect information, consisting in inferences about the structure from the character of processes which appear on the outputs of the modelled system. We can utilize here only in a small degree classical control theory, because typical technical circuits have rather different properties from already existing models of biological structures. Therefore, it is necessary to have some more basic information about the processes in these structures; we may obtain this information from the observation of circuits containing neuron models.

The utilization of the information of the first kind is very simple, but it is not so with the indirect information, where it is necessary to combine some exact information about the processes in nonlinear structures with intuitive interpretation of the results of the experiment.

First of all we should consider the sorts of structures we have to deal with, and methods of their identification and analysis. Then the problem of stability of the processes involved shall be briefly discussed.

From the description of Dewan given in the preceding paper it follows that we have to do here with a system which has the following properties:

1. The system is composed of many mutually interconnected feedback loops.
2. The system is strongly nonlinear because it is composed of threshold elements with saturation.
3. The system operates with pulse signals, and includes integrating circuits.
4. There exist in the system reciprocally interconnected centers which mutually inhibit each other.

In spite of the fact that all these properties are found in many technical arrangements, such as automatic control systems, their role in these arrangements is rather different from that which they play in the nervous system. This fact will be clarified in our further considerations. In our further considerations we tried to avoid mathematical description, and we have utilised qualitative, mostly graphical analysis. Such a method of analysis is indispensable, because of the lack of an appropriate mathematical method for the identification of neuron-like structures.

SOME PROBLEMS OF IDENTIFICATION OF STRUCTURES COMPOSED OF IDENTICAL ELEMENTS

As it was stressed in the introduction, the solution of the general problem of identification of structures meets essential difficulties and requires the introduction of a great number of assumptions taking into account the actual properties of the nervous system. It is also necessary to specify which values are given and which ones must be determined or assumed.

The number of inputs and outputs is as a rule determined in advance, and the general problem consists in inserting between them a suitable structure with a minimal number of elements (Fig. 1). Since the solution of such a problem is rather difficult it should be divided into two parts. The first part consists in determining the connections between elements of the modelled system without taking into account external inputs and outputs. These connections determine the processes which can occur in the system. The second part of the problem consists in determining the points of inputs and outputs. It is easy to see that the best situation for the identification of the system is when we have access to input and output of all elements. This means that

$$i = j = k,$$

where:

i — number of inputs to the system,
j — number of outputs from the system,
k — number of elements.

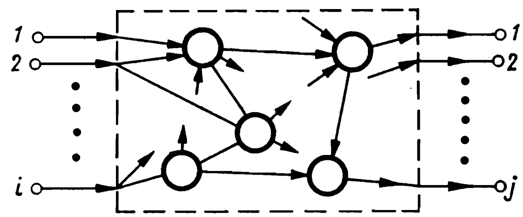

Fig. 1. Definition of a structure which is inscribed in a system having i inputs and j outputs.

Such system may be called a system with full access. One of the aims of modelling is just to obtain an arrangement with full access. Such a situation is, however, very rare in physiological investigations.

Some simplifying assumptions, especially concerning piecewise linearization [1], may allow the establishment of the structure on the ground of suitable measurements at all inputs and outputs.

Entering into the problem of modelling a part of the nervous system, we shall accept the following simplifying assumptions concerning its organization.

1. The structure forms a whole in the sense that every element is directly or indirectly connected with all other elements.
2. All connections are unidirectional.
3. Only one connection may exist in a given direction between any two elements.
4. Connections may ramify, and summation of signals occurs in the elements.
5. The number of inputs and outputs in every element is not limited.
6. All outputs from an element are identical.
7. Loops containing only one element are not taken into account.

The class of structures so defined is described in the theory of the so-called directed graphs, and some considerations concerning those graphs may be found in the paper of Harary (1955).

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[1] Piecewise linearization consists in the substitution of a nonlinear characteristic of an element by a characteristic which is composed of pieces of straight lines.

Examples of such structures for $k = 2$, 3 and 4 are given in Fig. 2. It is easy to notice that in each of these structures different processes, or different kinds of data processing (for a suitable combination of inputs and outputs) may (but not must) arise.

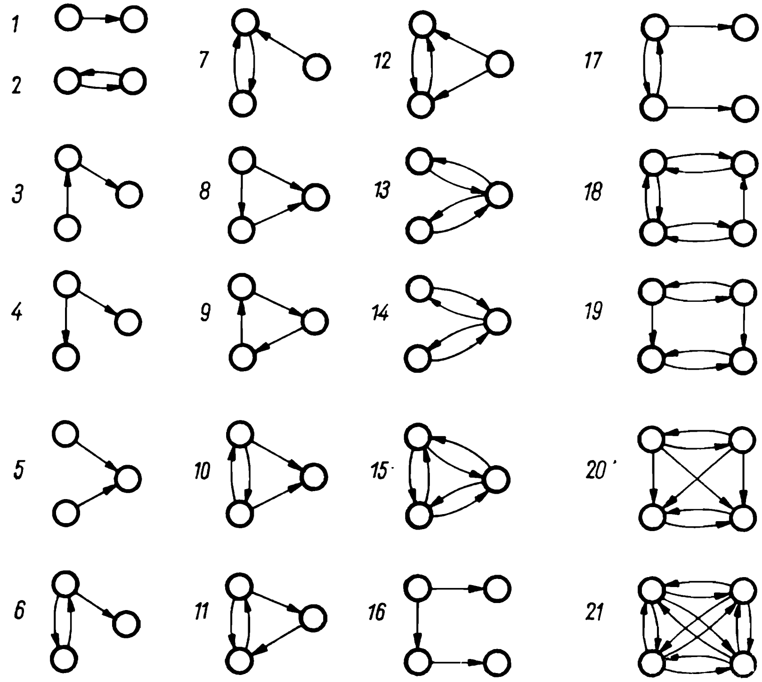

Fig. 2. Examples of structures containing two or three elements (full assembly), and some examples of structures containing four elements.

The number of different structures n which may arise from a given number of elements may be calculated with help of the formula which is given in the paper of Harary. This formula is very complicated, and the calculation of the number of structures n needs some additional operations. In Table I the results of calculations [2] as well as (for comparison) the values of $k!$ and k^k are given.

As we see from this table, the increase in the number of structures n, is extremely fast, much faster then the increase of the functions $k!$ and k^k which are known to be fast increasing functions. For each of these structures there also exists a correspondingly increasing number of input and output connections. The systematic investigation of all structural

[2] The suitable program for digital computer and appropriate calculations was done by mgr ing. Tyszko.

combinations for greater numbers of elements is practically impossible even with help of fast digital computers, the more so that the investigation of each structure takes relatively much time. Therefore, it is necessary to look for further rules for the selection of those structures which may be interesting for us. Such rules are:

Table I

Number of elements	Number of structures	$k!$	k^k
k	n		
2	2	2	4
3	13	6	27
4	199	24	256
5	9364	120	3125
6	1530843	720	46656
7	880471142	5040	823343
8	1.79247395×10^{12}	40320	1.6777216×10^{6}
9	1.30261617×10^{16}	362880	3.87420489×10^{8}
10	3.4124740×10^{20}	3628800	10^{10}

1. The existence of some symmetry in the processes which is the result of structural symmetry. In that case we are interested only in structures having appropriate symmetry of connections.

2. The existence of specific phenomena (such as self-oscillations) resulting from the existence of specific connections (for example feed-back loops).

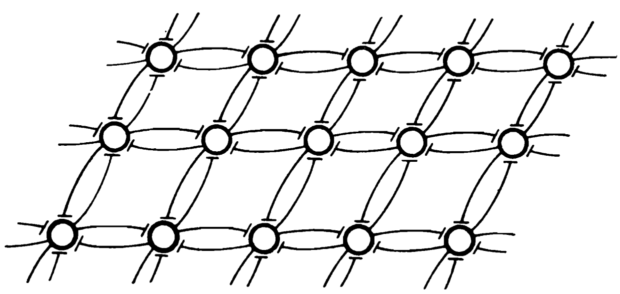

Fig. 3. An example of a one layer net with lateral inhibition.

Extreme cases of symmetry are homogeneous structures where every element is connected with its neighbours in an identical way. This is so in the case of stratal nets with lateral inhibitions (Fig. 3). Symmetry of connections is usually easy to detect by suitable measurements. In the system under investigation we may notice the symmetry of activity of FCS and ~FCS (see Gawroński and Konorski 1970, Fig. 8).

Utilization of the second rule is much more difficult and requires a good knowledge of the dynamics of the pulse threshold circuits.

Looking through the examples of structures which are given in Fig. 2 we may notice that the structures with loops containing two elements (Fig. 4) are of frequent occurrence. One can show that the statistical probability of such feedback connections increases quickly with the increase of k.

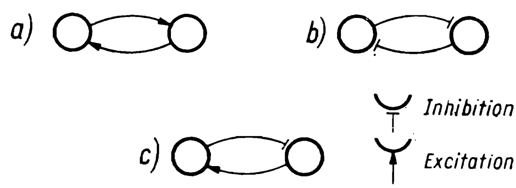

Fig. 4. Connection diagram of a loop with *a*, excitatory, *b*, inhibitory, *c*, mixed influences.

If we find, for example, that the system contains two pairs of elements mutually connected and only the first pair influences the second one, and only in a symmetrical way, then in the course of successive eliminations we may notice that from among 199 structures composed of 4 elements, only structures 19 and 20 in Fig. 2 are possible. Such considerations enable us to select a narrower subclass of structures which must be taken into account.

SOME PROBLEMS CONCERNING STABILITY OF NEURAL STRUCTURES

One of the important reasons for the application of modelling of particular systems is the study of the conditions and range of their stability. It is known from circuits theory that if in a given structure there exists a positive feedback loop with amplification greater than one, then a process ocurring in that loop increases up to the saturation level. We are interested here in two particular cases:

1. The positive feedback leads to the production of some rhythmical oscillations having the shape of pulse trains of a definite length.
2. The positive feedback leads to a steady state when some elements reach saturation level.

Both cases may have physiological significance. They correspond to instability of the system in the meaning of the classical Liapunoff-Poincaré definition. However, it should be noted that the operation of the model may still reflect some actual nervous processes. Only when there appear in the model such oscillations or steady saturation which are not observed or even not possible in physiological systems, can we say that the model is not adequate, due to its instability.

We observed such a situation in Dewan in the course of modelling the principle of the dependence of the intensity of the FCRs on the strength of the CS, when the connection weights between H and ~H, and F and ~F were too great, when the excitation levels ΣHCS and ~T were too high, and the connection between ~F and H was too strong. Then trains of oscillations appeared which ended in so strong an excitation of ~F that it could not be overcome even by strong FCSs.

In the course of modelling of neuron like nets particular attention should be given to ambiguity of solutions which may appear as a result of instability of the system (Variu 1962, Furman 1965). For example, depending on small random influence one of several possible processes can arise. In terms of the theory of stability we have to do here with the bifurcation point of a solution of a nonlinear equation. After the crossing of this point a non-uniqueness of a solution appears. In Fig. 5

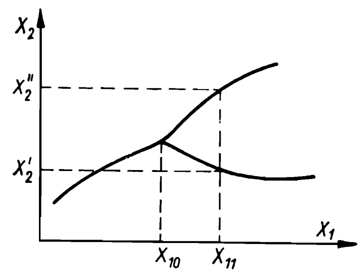

Fig. 5. Bifurcation of a solution of an equation describing an unstable system.

we have an example of a solution (x_2) of an equation which is a function of an independent variable (x_1). When the variable x_1 crosses the value x_{10} the split of the solution takes place, and for $x_1 = x_{11}$ two values $x_2 = x_2'$ and $x_2 = x_2''$ are possible.

Situations of this kind belong to the undetermined behavior of the system and so far they have not been taken into account in modelling of the nervous system.

Some evidence about the unexpected consequences of instability in neural nets is given in the study by Decowski (1968) concerning modelling of a single loop in a neuron endowed with the properties of pulse generation, absolute and relative refractory period and delay (propagation time) (Fig. 6). At the first glance it seemed that the assumed ideal delay and threshold characteristic would lead to the permanent circulation of a single pulse applied to the neuron (lowest input in Fig. 6). Similarly the application of two and more pulses at intervals t_{i_1}, t_{i_2}, t_{i_3} ... greater than refractory period, but shorter than the delay time, would lead to the circulation of two and more pulses in the loop. It turned out, however, that in this condition an unstable situation arises and the intervals t_i between the pulses gradually change, leading either to the decay of the pulse circulation, or to the settlement of pulses into a definite frequency. It follows that in such a loop pulse trains endowed with a definite pattern of pulse intervals cannot be permanently reverberated.

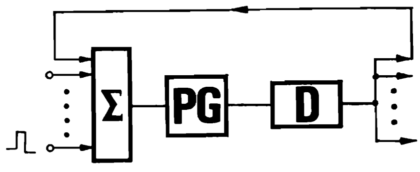

Fig. 6. A single feedback loop containing one neuron. Σ, summing circuit; *PG*, pulse generator; *D*, delay.

To end these considerations it may be noted that the integrating circuits which have relatively great as well as very small time constants (see the description in the preceding paper) may cause the growth or decay of the processes produced by the instability of the system to be very slow and comparable with the slow changes caused by thermal influences.

INTEGRATION AND PULSE PROCESSES

One of the specific properties of the nerve net model is that it is composed of a number of pulse generators separated by integrating circuits and delay lines. The pulse generator corresponds to that part of the cell membrane (usually close to axon hillock) where, due to the resultant depolarization, an action potential is generated, whereas integration takes place generally in the synaptic region and may be observed when investigating subthreshold phenomena.

In automatic control theory several methods of investigation of pulse systems based on difference and difference-differential equations and so called z transformation have been developed. But these methods are limited to linear circuits, and therefore, they cannot be applied in investigations of neural structures. For that reason we shall present here some comments concerning qualitative aspects of the processes in the simplest pulse networks with integrating circuits. These comments may be useful in the interpretation of the results in further papers of this series (Konorski and Gawroński 1970ab).

To begin we shall consider the transmission of the pulse trains of various frequencies, through a single neuron, taking into account integration and threshold characteristic. The block diagram of connections is shown in Fig. 7*a*, with the processes occurring at the input, after the

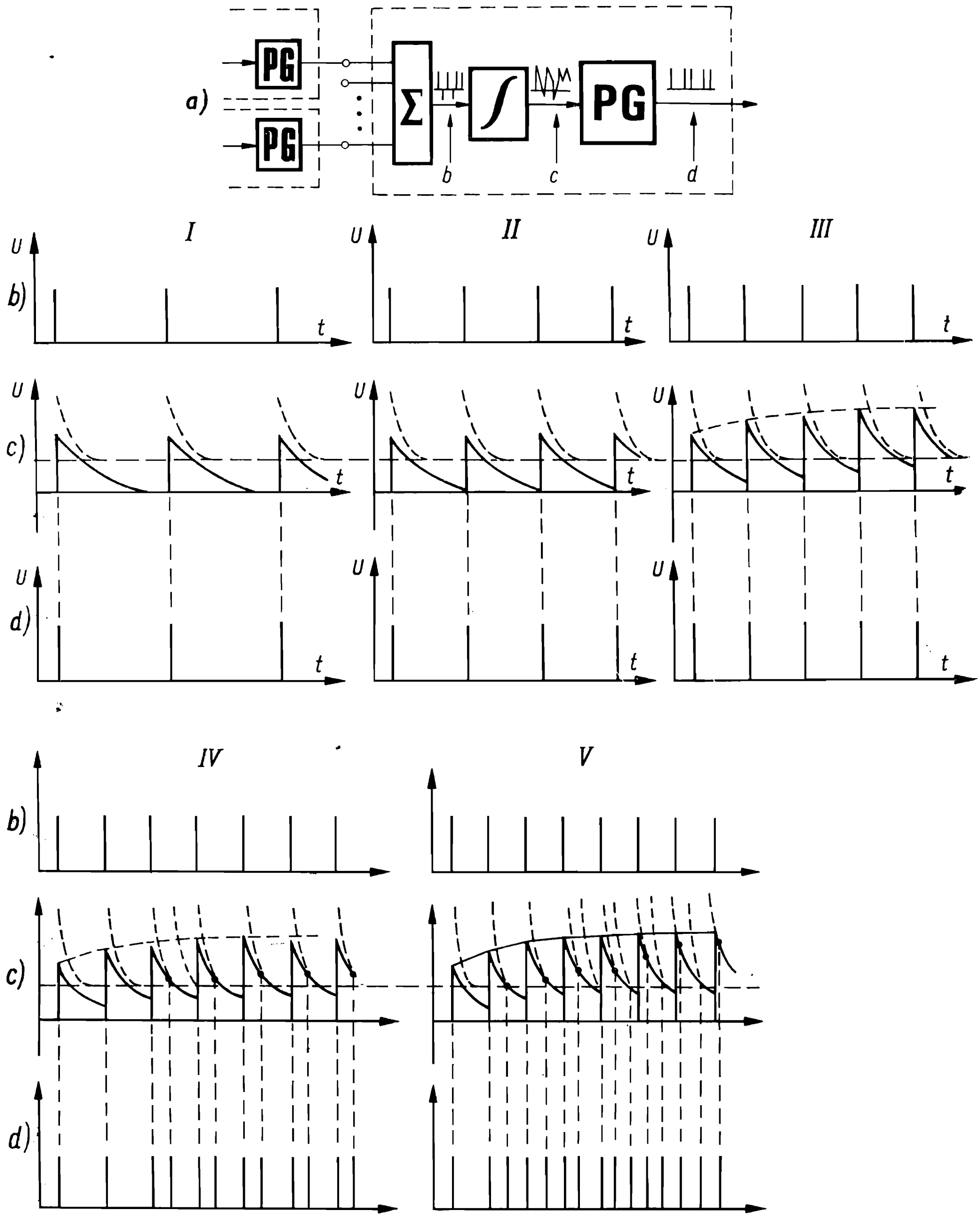

Fig. 7. The transmission of pulse trains through a single neuron with integration circuit. The case of large input weight and high threshold. *a*, The block diagram showing the points of measurements of processes for *b*, *c* and *d*; denotations as in Fig. 6; ∫, integrating circuit. *b*, Pulses exciting the neuron; on successive drawings from I to V — examples of lower and higher pulse frequency are given. *c*, Excitatory signals after integration; the falling dashed lines denote the threshold change after each excitation (relative refractory period); the horizontal dashed line denotes the steady threshold value. Pulse generation occurs when the dashed falling line (instantaneous threshold value) crosses the continuous line (resultant exciting value). *d*, Pulses in the output of the pulse generator.

integration, and at the output drawn in Fig. 7*bcd* respectively. The dashed lines in Fig. 7*c* show the changes in the threshold value of the neuron after each excitation (the horizontal dashed line denotes steady value of the threshold). The generation of the pulse takes place, as we know, in the moment of the crossing of the instantaneous value of the threshold with the instantaneous value of the exciting voltage applied to the neuron. As we see from the successive examples given in Fig. 7 (drawings I to V) the output frequency is initially proportional to the input frequency (drawings I, II and III). But when the influence of integration causes the increase in the average value of the exciting voltage, we notice a faster increase of the output frequency. In drawing IV, all input pulses beginning from the third one cause the generation of an additional output pulse. Starting from some sufficiently great value of the input frequency a constant surpassing of the threshold occurs, and the output frequency is close to the maximal value which is determined only by absolute refractory period (drawing V). Fluctuations of the exciting voltage cause some variations in the intervals between successive pulses and the corresponding histogram should have a two-modal characteristic. A resultant characteristic of the output frequency as a function of the input frequency is given in Fig. 8. The described processes cor-

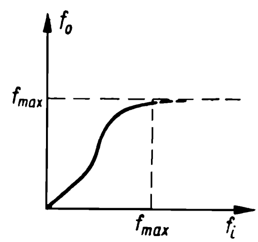

Fig. 8. The approximated characteristic of the excitation for the case given on Fig. 7; f_i, input frequency; f_o, output frequency.

respond to the case when the neuron has high threshold and also great input weight (a single pulse is able to excite the neuron). The first part of the characteristic is linear but then it rises much faster and afterwords a flat part, corresponding to the state of saturation, occurs.

For comparison let us consider the analogous processes in a neuron with a much lower threshold (Fig. 9). Here every input pulse produces two output pulses. With the increase of frequency of the input pulses two phenomena are observed. One consists in a proportional growth of frequency of the pairs of impulses, the other one consists in the diminution of the intervals between the pulses within each pair, due to the increase of the average value of the excitation voltage. When the histogram method is used these phenomena become even more manifest. With further increase of the frequency of input pulse trains each pulse generates three output pulses. Still further increase leads to the effect of saturation with the resultant characteristic of the element similar to that shown in Fig. 8.

As a second example we shall consider the effect of the application of two trains of pulses (through two inputs), the first train consisting of excitatory pulses and the second one of the inhibitory pulses. First, let us assume that the time constant for excitatory pulses is the same as

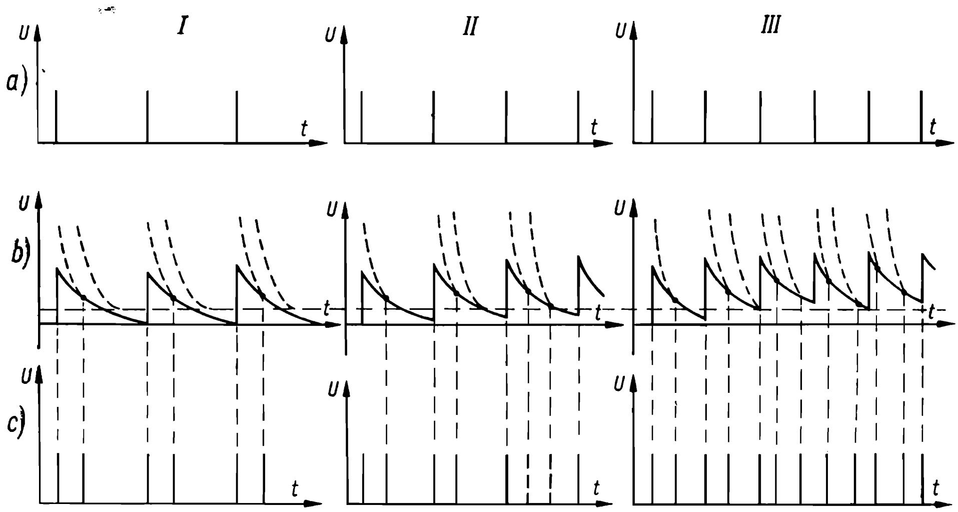

Fig. 9. The transition of a pulse train through a neuron for the case of smaller threshold. Explanations for *a*, *b* and *c* as for *b*, *c* and *d* in Fig. 7.

that for inhibitory pulses and is relatively small in comparison with intervals between pulses. An interesting phenomenon appears here consisting in the dependence of the output processes on the order of the time relations between excitatory and inhibitory pulses.

The influence of the temporal relations between negative and positive pulses is shown in Fig. 10. When, in the case of constant pulse frequencies, the positive (excitatory) pulse precedes the negative (inhibitory) pulse by a shorter interval than it precedes the next positive pulse (Fig. 10, drawings I and II), there is a negligible or no influence of the inhibitory pulses. Only when the negative pulse closely precedes the positive one, can its influence be seen; however, such a situation occurs rather seldom — especially for small pulse frequencies. For higher pulse frequencies, the occurrence of this relationship is more probable. Drawing III in Fig. 10 illustrates this situation by showing pulse frequencies with negative pulses closely preceding positive ones; the influence of the inhibitory pulses is clearly seen in the irregular output. It can be shown that for higher input frequencies very slow but well marked fluctuations in the distribution of output pulses may be caused by only small random fluctuations of input frequency.

Another situation occurs when the frequencies of inhibitory and excitatory pulses are markedly different. Such a situation is shown in Fig. 11. It appears that the small mutual displacements between the pulses

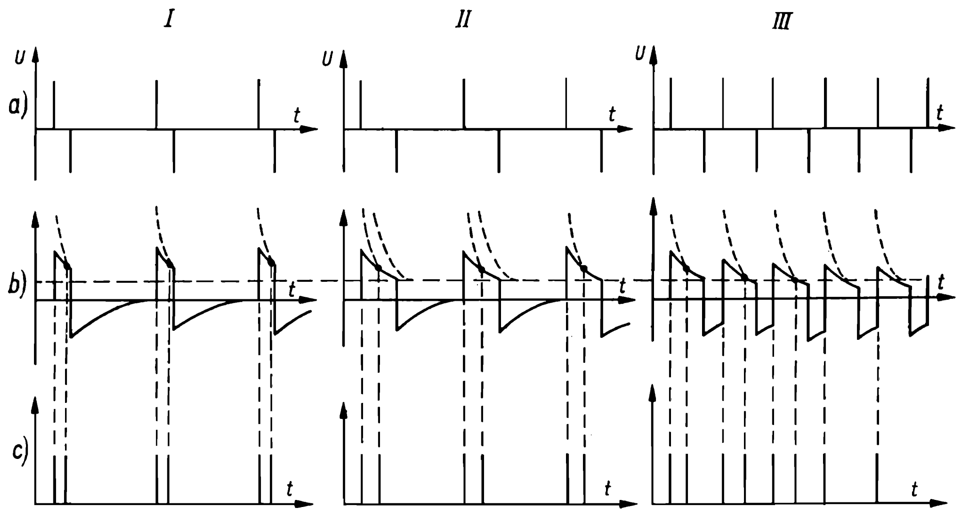

Fig. 10. Summation of excitation and inhibition when the pulse frequency is relatively low (I and II), and relatively higher (III). In each case, positive and negative pulse frequencies are equal. Explanations as in Fig. 7 and 9.

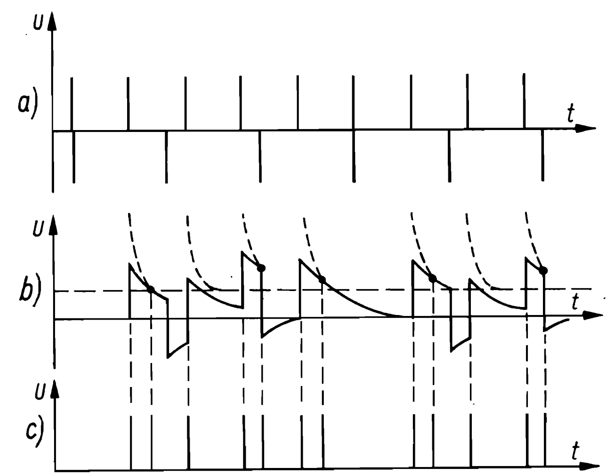

Fig. 11. The resultant effect of excitation and inhibition by pulses with different frequencies.

may cause either the clear manifestation, or full abolition of the effects of inhibitory pulses. In the output we observe, then, grouping of the pulses which may form very different patterns. These patterns may be much more complicated in comparison to that presented in Fig. 11, when the inhibitory and excitatory pulses are applied to a neuron from many sources.

In examples so far presented we assumed that the neuron is inhibited or excited from a few sources, and the weight from each source has a great value. In physiological terms this may mean that the messages from one neuron to another are transmitted through a great number of parallel synapses. Quite a different situation occurs, however, when the signals exciting a neuron come from many neurons and the weight of every input is relatively small. The resultant signal is then composed of many mutually asynchroneous pulses. When these pulses are transmitted through integrating circuits we get a fluctuating curve with small amplitude of oscillations. As we see in Fig. 12, slight changes of the threshold or of the resultant excitation may lead to surpassing of the

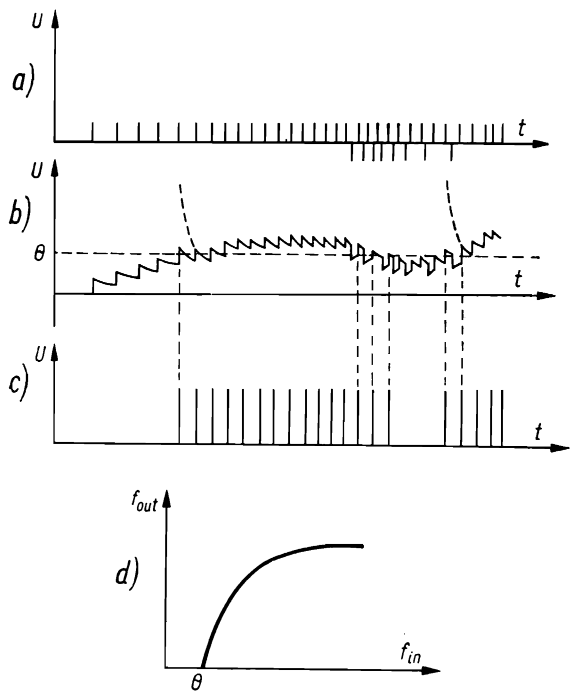

Fig. 12. Summation of excitation and inhibition in the case of many inputs with small weights. Explanations for *a*, *b* and *c* as for *b*, *c* and *d* Fig. 7. *d*, The resultant characteristic of the elements.

level of the pulse generation. The first segment of the characteristic corresponding to that situation (Fig. 12*d*) has then a steep slope, but the next one is much flatter and has an apparent bend resulting from the characteristic of the relative refraction (Gawroński 1970).

When analysing the processes given in Fig. 10 and 11 one can see that the effect of inhibition is revealed only when the frequency of the inhibitory pulses is close to maximum; as a rule the inhibitory effect rises suddenly. Moreover, at medium levels of inhibition, the processes are unstable and small changes of mutual positioning between pulses are sufficient either to reveal or to remove the influence of inhibition.

For comparison we shall consider a second case when the time constant of inhibition (that is the time constant of the filter transmitting inhibitory signals) is much greater than the time constant of excitation.

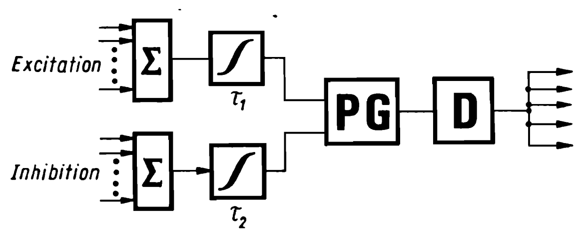

Fig. 13. A model of the element with different time constant for inhibition and excitation. ∫, integrating element; *PG*, pulse generator; *D*, delay.

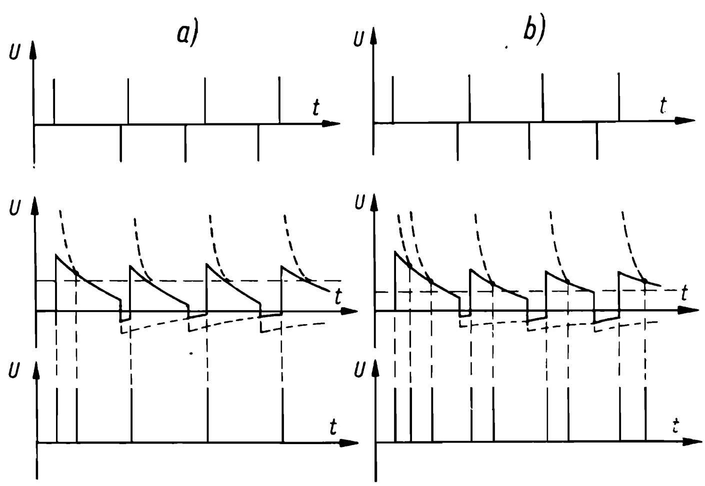

Fig. 14. The influence of inhibition in the case of a large time constant for inhibition. Explanations as in Fig. 7 and 8. *a*, An element with high threshold. The appearance of the inhibitory pulses caused the disappearance of every second pulse after each excitation. *b*, An element with small threshold, the appearance of inhibition diminished the frequency by 1/3.

The block diagram of such an element is shown on Fig. 13. According to a good deal of physiological evidence (Eccles 1964, Kostiuk 1965, Wartanian 1966) such a situation does frequently occur in presynaptic inhibition. In Fig. 14 the effects of inhibition in a case of high threshold (*a*) and low threshold (*b*) are shown. Unlike the processes presented in Fig. 10 and 11 the effects of inhibition are here more considerable and less dependent on mutual displacements between the pulses. It can be shown that the characteristic illustrating the mean effect of inhibition is much flatter for a large time constant (Fig. 15*a*) than for a small time constant (Fig. 15*b*).

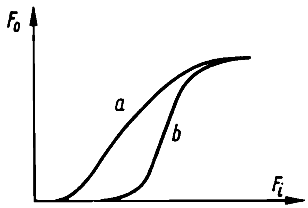

Fig. 15. The characteristics of an element showing the influence of inhibition for the case of large (*a*) and small (*b*) time constants: F_i, the frequency of inhibiting pulses; F_o, output frequency.

All these considerations induced us to use in Dewan integrating circuits with a time constant of about 100–200 msec in those connections where inhibitory signals are transmitted, and only then the reasonable results of modelling were obtained.

SOME PROBLEMS CONCERNING THE DYNAMICS OF RECIPROCALLY CONNECTED CENTERS

Many processes observed in the nervous system, such as sudden transitions from excitation to inhibtion, antagonistic relations between centers, and the phenomena of hysteresis point to the importance of reciprocally interconnected centers (Fig. 4*b*). According to the rules proposed by one of the authors (Konorski 1967), in our model of the alimentary system there also exist reciprocally connected subcenters. For that reason it is necessary to consider the properties of such systems, assuming that every subcenter (or element) has the properties described in the preceding paper (Gawroński and Konorski 1970).

At the beginning we shall consider the simplified situation in which only summation effects and threshold characteristics of elements are taken into account, while their pulse activity is neglected (in Fig. 16). The possibility of the application of some additional signals to each element was also taken into account. They may be either identical or different for each element. Such systems are studied also in electronic circuit theory, because multivibrators commonly used in pulse circuits

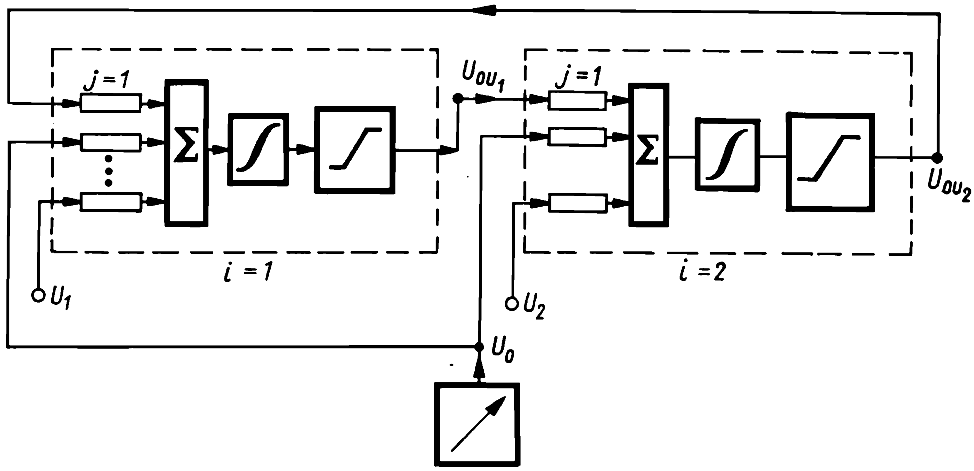

Fig. 16. Connection diagram for two threshold elements antagonistically connected; U_0, constant signal applied to both elements; U_1 and U_2, the signals applied accordingly to the inputs of the first and second element.

and digital computers have a similar construction. However, in electronic circuits these systems are controlled in a different way, and other properties are utilized. The processes involved in these systems are described with help of nonlinear differential equations, the solution of which encounters considerable difficulties. Mixed analytic-graphical methods are often used for that purpose (Gawroński 1962ab).

The properties of the system under discussion depend on its resultant amplification. For each element i and input j there exists a resultant amplification for small increases, that is the ratio:

$$\frac{\Delta U_{\text{out}}}{\Delta U_{\text{in}}} = k_{ij} = V_j k_{ri},$$

where:

ΔU_{cur}, denotes small increment of the voltage in the output of the element i,

ΔU_{in}, denotes small increment of the voltage in the input j of the element i,

V_j, the weight of the input j,

k_{ri}, the slope of the characteristic of the element ($i = 1$ or 2 in our considerations) in the actual point of operation which was established by the average values of all signals applied to the element.

The amplification k_{ij} may be either positive when the increments ΔU have the same sign or negative when the increments are of opposite signs. The latter situations occurs for inhibitory signals.

It follows from the principal theorems on feedback circuits that if the resultant amplification for both elements is smaller than one, that is if.

$$k = k_{1,1}k_{2,1} < 1$$

(it was assumed that $j = 1$ as in Fig. 16), then the system is stable, and all processes are uniquely determined by input signals. For simplification we shall assume that the system is symmetric that is:

$$k_{1,1} = k_{2,1} = k_0^2$$

Let us consider the steady state, that is the situation in which either no changes or very slow changes occur in the input. Let us also assume that the static characteristic has the shape given in Fig. 17, and the operation point is placed on the lower horizontal segment at a value of Θ on the abcissa.

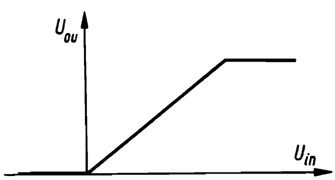

Fig. 17. The simplified characteristic of the threshold element with saturation.

By application of various signals to the antagonistic system under consideration we generally obtain different processes from those obtained in a single element. Only in those cases in which the signal is applied to one element of the system (the voltage U_1 in Fig. 16) does the corresponding process at the output of that element lead to the greater and greater inhibition of the second element.

More interesting is the situation when a constant identical voltage is additionally applied to both elements (Fig. 18). This voltage is choosen

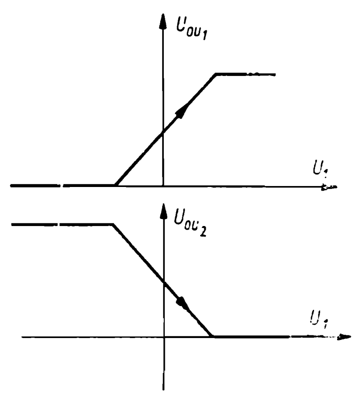

Fig. 18. The characteristics of the system composed of two antagonistically connected elements for the case $k_0 < 1$.

so as to move the operation point to the middle point of the linear segment of the characteristic of each element. Two significant changes can then be noticed. Firstly, the increase of the voltage in the input of the first element will now cause the decrease of the output voltage of the second element; analogous changes, but in opposite directions, appear in the output of the elements. Secondly, the slope of the changes of output of the first element shall now be greater, because the changes (of the same sign), which come from the second element, shall be added to the changes of the voltage U_1 (see Fig. 16). This occurs because we have to do here with positive feedback due to two changes of the signal sign. As we know from the basic formula for feedback loop the resultant amplification is now equal to:

$$k_r = \frac{k_{1,1}\,k_{2,1}}{1-k_{1,1}\,k_{2,1}}.$$

This amplification k_r is greater, the closer to one is the value $k_{1,1} \cdot k_{1,2}$ (in our case k).

For the limiting case $k_0^2 = 1$ we get an infinite slope, that is the vertical characteristic of the system. This means that any small increase of the voltage at any input shall cause an avalanche process which shall end with full saturation of one element and full inhibition of the other. The transition time may be calculated with help of some approximate formula (Gawroński 1962b) and depends on the time constants of the integrating circuits.

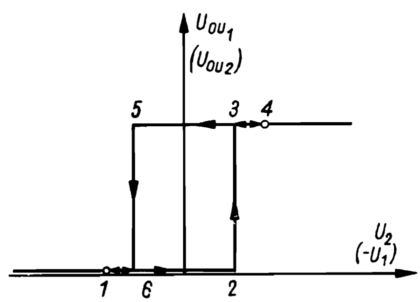

Fig. 19. Characteristic of a system composed of two antagonistically connected elements for the case $k_0 > 1$. The characteristic has the shape of hystheresis loop. Explanation in text.

For the amplifications k_0 greater than one, at least one of the elements is inhibited or saturated. When to both elements the above mentioned medium voltage of equal value is applied, we shall obtain the situation presented in Fig. 19.

Let us assume that under the influence of previously applied signals one of the elements (say the first) is in the saturation state (point 4) and, owing to the great amplification ($k_0 > 1$), the second element is fully inhibited (point 1 in Fig. 19). The transition to the opposite state occurs only under the influence of a sufficiently great signal applied to one input. We assume here that it is the positive signal U_2 applied to the second element. That signal must compensate the inhibitory signal from the first element and shift the operation point from point 1 to point 2 where the condition for sudden change of state appears. Then the operation point goes through point 3 to point 4. Now the same change of the voltage U_1 or the opposite change of U_2 causes the shifting of the operation point from 4 to 5; thereafter this point jumps suddenly from 5 through 6 back to our starting point 1. We get the typical hysteresis loop. The width (distance from point 6 to 2 or from 3 to 5) of this loop is the greater, the greater is the resultant amplification of the system. This means also that for greater amplification it is more difficult to change the state of the system. Such a system is often called a "hard system" as opposed to a system having the amplification $k_0 < 1$, when a slow and controllable transition from the saturation to the inhibition state of one element or from inhibition to saturation of the other one is possible. The latter system is often called a "soft system". In the system under investigation the conversion from the soft system to the hard one was done with help of multiplying inputs described in the preceding paper. For example, the system F— ~F was a soft system for small values of hunger (Fig. 8 of that paper), but for great values of hunger, when the amplification was greater, we obtained a hard system with an evident hysteresis loop.

Comparing the F- ~F system with the system presented in Fig. 16 we may note a difference in the manner of excitation, because in the place of a constant signal U_0 asymmetrical signals were applied. They are of two kinds:

1. While investigating unconditioned reactions the transition from the excitation of ~F to the excitation of F occurred by switching off one signal (~T), and switching on a second signal (T). For greater values of T and ~T it was impossible to discriminate whether the system was soft or hard because in both cases a fast transition from the excitation of F to the excitation of ~F took place.

2. While investigating conditioned reactions various values of FCS were applied to the F center. At the same time the signal from ~T constantly excited the ~F center at medium or close to maximal values, depending on hunger level. In such conditions processes similar to those described above were obtained, and it was easy to estimate whether the system was hard or soft (see Konorski and Gawroński 1970a).

Similar considerations are true for the H- ~H system, which also could operate as a soft or a hard system, depending on the level of satiation (Sat).

To end, we shall take into account the pulse operation of the elements, neglected in the previous considerations. The influence of the pulse operation depends on time constants of the integrating circuits linking the reciprocally connected elements. If the time constants are large (in comparison with pulse intervals) then the general behavior of the system is similar to the nonpulse (pure analogue) system.

A difference between the two systems appears only, when the time constant of the integrating elements are comparable to pulse intervals at lowest frequencies. This difference is well-marked when both centers operate together (soft operation) and are under the influence of excitatory and inhibitory signals. As we know from the considerations of the preceding section, we observe then interesting processes consisting in rhythmic changes of the pulse intervals, that is in the grouping phenomenon. This phenomenon may be intensified due to feedback and delays, in particular in integrating circuits. The resultant pulse distribution may be very complicated especially when the circuit is excited by another center in which grouping also exists.

The analysis of such processes, even if only graphical, is in general very difficult, and it would include a number of varieties. An example of a relatively simple case of pulse grouping in the antagonistic system is shown in Fig. 20.

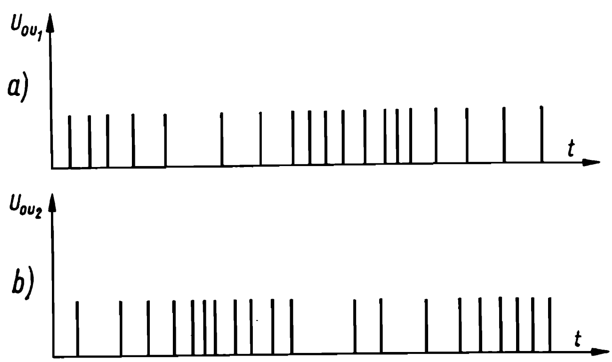

Fig. 20. An example of the process in an antagonistic system with evident grouping effect. *a*, The processes at the output of the first element. *b*, The processes at the output of the second element.

Obviously we observe still more interesting and complicated patterns of pulses when two systems of reciprocally connected centers cooperate. Such was the case in Dewan with H– ~H and F– ~F centers. It must be stressed that partial symmetry of a structure (for example in structure number 18 on Fig. 2) involves partial symmetry in the patterning of pulse trains. Although it is possible to imagine a method of identification of the structure on the basis of the details of pulse distribution patterns, this is a difficult task and requires the elaboration of more precise and more effective methods of analysis of pulse processes in neural structures.

CONCLUDING REMARKS

We must realize that in spite of the considerable complexity of our model it is a very simplified representation of the actual structure of the alimentary system. One of these simplifications is the replacement of a great number of neurons taking part in a center by a single element complemented with integrating circuits. This leads to the neglection of many interesting phenomena which may appear in structures containing many elements. If such structures are for example endowed with a certain symmetry some rhythmic processes may appear in them, which may have a fundamental influence on the resultant operation of the center.

From the considerations concerning processes in pulse circuits which were presented in the preceeding sections it follows that the problem of pulse grouping which may appear in very complicated pulse patterns must be treated with great caution. In particular the statement that by means of these patterns a great amount of information may be transmitted from one center to another, may lead to inappropriate interpretation of the manner of signal coding (Konorski and Gawroński 1970ab). It was already shown in sections 4 and 5 that particular patterns depend on small changes of parameters and excitations, and for this reason they are very labile. It is very difficult to assume that all elements and processes in the nervous system are so stable that they would not cause some changes in fine displacement of pulses in the pulse patterns. This issue must be also taken into account when elaborating methods of physiological data processing with help of digital computers.

In the course of study of our model it appeared that the electronic arrangements which were used here have some imperfections which must be eliminated in more detailed investigations, especially when still larger structures are modelled. First of all, the stability of output processes must be improved and in particular the slow changes of output frequency due to thermal influences must be eliminated. It may be noted that the influence of such slow changes may be similar to changes in pulse patterns which reflect processes in the original system. Such changes play a considerable role in modelling of adaptation, learning and short-term memory mechanisms.

The second imperfection which must be eliminated is the difficulty in controlling and matching the parameters. First of all one must secure successively: (i) ease in matching of input weights; (ii) ease in setting up threshold excitation; (iii) the possibility of regulation of integration time constants.

Nets with such properties would be very flexible tools for model investigations.

The analysis and modelling of nerve nets which has been done so far shows that the following procedure of modelling is reasonable:

1. On the basis of neurophysiological data and hitherto existing experience in modelling, the general structure of the model and its parameters must be determined.

2. The detailed identification of the structure and parameters must be accomplished so as to replicate all known results of the neurophysiological experiments and principles of activity.

3. Then it must be estabilished which properties of the system are most important and which may be omitted as insignificant.

4. On the basis of these results a mathematical model should be determined which would give a solution without loosing any important features of the modelled system.

As it follows from our succeeding papers (Konorski and Gawroński 1970ab) in our modelling of the alimentary system we have reached successfully the first three stages. This made our model amazingly similar to the original as far as the principles of its activity are concerned. The fourth stage has not yet been achieved, and this is a task which would certainly require some new mathematical methods which have not been developed so far.

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