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

II. TECHNICAL DESCRIPTION OF THE ARRANGEMENTS INVOLVED IN MODELLING

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GENERAL REMARKS

In the preceding paper of this series (Konorski and Gawroński 1970a) a concept of general organization of the central alimentary system of higher animals was presented. In the present paper we shall give a justification of the chosen method of modelling, as well as its technical description. The following paper (Gawroński and Konorski 1970) will be devoted to analysis of processes occurring in the models of that kind, especially in the systems containing reciprocally related centers.

At the beginning we shall briefly discuss the reasons which have inclined us to apply the modelling method for investigation of pure physiological phenomena, a method often arousing many doubts and controversies. As we may see from Fig. 3 of the preceding paper the system under discussion has a rather complicated structure, even if we take into account a number of simplifying assumptions. The processes arising in such structures are very complex depeding both on the properties of their elements and subsystems and on kinds and magnitudes of their mutual connections.

Proposing a concrete structure simulating connections between centers of the nervous system we are confronted with the following questions:

1. Whether the processes observed in the proposed structure can occur in physiological experiments.

2. Whether there arise in the model some processes inherently connected with its structure, that are not observed and even not possible in the modelled system.

3. Whether there arise in the model such processes that are not observed in the modelled system, and which should be experimentally verified.

It is necessary to get answers to these questions if we want to prove that the proposed scheme of organization of centers really explains known neurophysiological data and has no logical contradictions with the original modelled system.

As long as we have to do with very simple systems composed of two or three elements having simple properties, the answers to these questions are easily obtained by a logical, or simple mathematical analysis. Sometimes it is possible to employ some general methods of analysis from circuit theory. It appears, however, that we encounter essential limitations very soon. One of these limitations is that connected with the nonlinear properties of elements of the system. In fact, the generally used mathematical methods are restricted to linear systems in which the superposition principle may be used.

Acceptance of such strong simplifying assumption would be in conflict with some essential properties of the nervous system, and would leave unexplained many important physiological processes (e.g. all rythmic processes). Accordingly, whenever we are confronted with a system which is too complex to be explained by applying a simple mathematical or logical analysis, the best tool for its understanding is constructing its model.

When a model of a given physiological system is already established, another important question arises, as to whether other models, in particular more simple than that which was adopted, are suitable for simulating a given physiological system. If such other models lead to some different conclusions than that primary adopted, and if there are no experimental facts veryfying which conclusions are correct, then such modelling study may greatly contribute to promoting the investigation in the given field.

At the present stage of the development of the modelling methods, we have at our disposal two possible procedures. The first consists in using universal digital computers, the second one consists in the construction of special arrangements composed of standard elements which are interconnected according to the structure to be studied. Each of these procedures has some advantages and disadvantages, and the field of their application does not overlap entirely.

The application of digital computers needs only preparation of a suitable program, and the time of calculation is in comparison to the programing time extremely short. But in the course of modelling it is usually necessary to introduce many changes of parameters depending on the intermediate results. The whole procedure is often rather troublesome and does not help in understanding the dynamics of the modelled system.

The second procedure is free of the above mentioned disadvantages. It needs the construction of suitable elements (which shall be described later on), but they are not very expensive and may be used in many problems. By employing elements with the appropriately regulated properties which can be interconnected in many ways, we can relatively easily match the parameters of the system so, as to obtain the desired results. Unlike digital computers where all processes are coded in the program, here it is possible to apply visual indicators (for example midget lamps) of the output values. Since every element or a group of elements corresponds to a concrete center of the nervous system, the experimenter relatively easily becomes familiar with the potentialities of the model and learns to match its parameters so as to obtain the appropriate results. For model investigations described in this series of papers a net composed of neuronlike elements constructed in the Laboratory of Bionics — Institute of Automatic Control was employed. This net was furnished with a few additional elements indispensable for proper modelling of the system under discussion.

THE PROPERTIES OF ELEMENTS

The appropriate choice of the properties of the elements used in the model is a kind of compromise. On the one hand it would be useful to model all known properties concerning the transmission and transformation in the nerve cells, on the other hand, if the model is too complicated and has too many regulations, it is difficult to set up appropriate working conditions. It may be supposed, for example, that if we analyze only the problem of cooperation of centers, and every center is composed of hundreds or thousands of elements, it is not necessary to take into account the pulse operation of each neuron, since the output may be expressed by a continuous function of the inputs supplied to the center. It has appeared, however, that the pulse operation of the elements evidently influences dynamic properties of the centers, a problem which will be discussed in detail in the next paper (Gawroński and Konorski 1970). Therefore, it was decided to use pulse operation for all elements in the model. On the other hand, we have not taken into account changes of the shape or amplitude of the pulses, in accordance with physiological data, and the operation of the integrating circuits in our model.

As a result of such considerations and our experience in modelling of neuronal structures we have chosen the following properties of the elements comprising the model (Fig. 1).

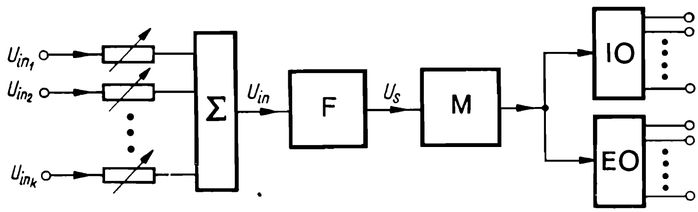

Fig. 1. Functional diagram of neuron models used in Dewan. Σ, summing element; F, averaging circuit where time summation is obtained; M, frequency modulated pulse generator; EO, excitatory outputs; IO, inhibitory outputs.

1. Every element has several (in our case ten) additive inputs. This means that the signals, arriving simultaneously at a number of inputs (each corresponding to a synapse or a group of synapses fed by one axon), give a resultant input signal denoted further by U_{in}. This phenomenon corresponds to the principle of spatial summation in neurons. The value of every input signal is multiplied by the coefficient determining its weight corresponding to the transmitting potency of the synapses. We can write that rule using the following simple formula:

$$U_{in} = V_1 U_{in_1} + V_2 U_{in_2} + \dots + V_k U_{in_k}$$

where:

$V_1, V_2, \dots, V_k$ — the weights of corresponding inputs,

$U_{in_1}, U_{in_2}, U_{in_k}$ — the signals applied to corresponding inputs of the element (Fig. 1),

k — number of inputs.

Each weight may be regulated with the help of a potentiometer.

2. The resultant signal is then applied to the averaging network (strictly speaking to the inertial network of the first order) which "smoothes" the input, as it happens in the synaptic region.

In electrical systems, this is equivalent to the transmission of signals through a simple circuit consisting of capacitance C and resistance R (Fig. 2*a*). In Fig. 2*b* a result of such averaging is shown. The degree of averaging may be characterized for example by the speed of the voltage decay after a sudden interruption of the input signal. That speed is determined by the time constant τ of the rise or the decay of the signal. In the described model of the neuron it was assumed that $\tau = 4$ msec, which is in the range of some data concerning the decomposition time of the mediator in the synaptic space. The above described procedure corresponds to the effect of temporal summation of the impulses impinging on the neuron.

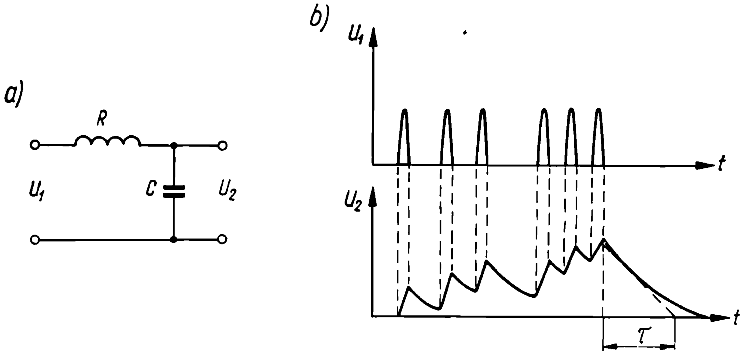

Fig. 2. Averaging of the processes with help of an RC — filter. *a*, Filter scheme: U_1, input signal; U_2, averaged output signal; R — resistance; C — capacitance. *b*, Illustration of the averaging effect when the input signal has a form of pulse train; τ, time constant of the filter.

3. The element generates frequency modulated pulses. This output of the element is characterized only by the instantaneous frequency of the generated pulses, the pulses having constant shape and amplitude. Maximum pulse frequency equals 1000 pulses per second; the pulse duration is about 0.5 msec, their amplitude is 10v, and their shape is similar to the shape of pulses in motoneurons.

4. Every element has a threshold characteristic (Fig. 3) with saturation. This means that the element generates pulses only when the resultant

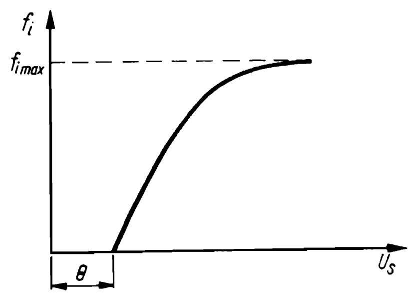

Fig. 3. Threshold characteristic of the element; Θ, threshold value; U_s, resultant stimulating signal; f_i, frequency of the pulses generated by the element.

excitation voltage U_s (Fig. 1) surpasses the threshold value Θ, and when the excitation voltage is sufficiently great, the pulse frequency does not surpass the definite value f_{max}. The value of the threshold may be regulated from 0.3v up to 6v. Owing to the averaging circuits described in point 2, we get the subthreshold summation effect.

5. Two kinds of outputs were used in our experiment and there were ten parallel outputs of each kind. On the outputs of the first kind we get excitatory signals. Since the transistor technique is used in the elements these signals are represented by negative pulses. The second kind of outputs gives rise to the inhibitory signals represented by positive pulses. From the neurophysiological point of view the first kind of signals depolarizes the membrane of the following neuron and the second kind of signals causes hyperpolarization of the cell membrane.

Twenty three transistors and twelve diodes were used in each element. This means that the scheme is rather complex, but owing to this we may have independent regulation of parameters over a broad range, and also some additional features concerning adaptation and memory, which were not utilized in this model.

The whole unit has a form of a cubic box (Fig. 4), on the upper side of which inputs, outputs, and regulations are placed as well as a special

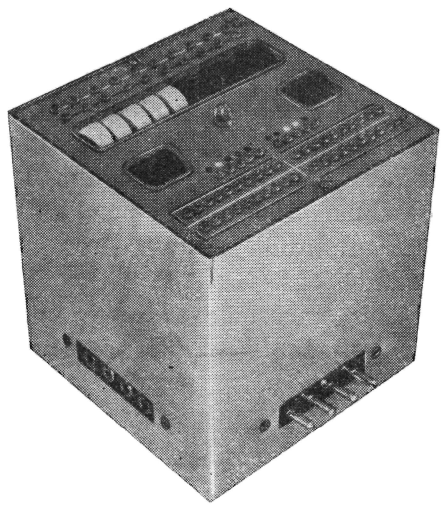

Fig. 4. Neuron model used in Dewan.

lamp. The intensity of light of this lamp is roughly proportional to the degree of excitation of the element. Contacts which are placed on the lateral sides serve for power supply connections either directly or through other boxes, when they are set up in a greater net.

As we see from this description, the elements imitate quite well the phenomena in single neurons, but they cannot serve directly for modelling processes in centers involving many neurons. For this purpose one should use many elements and apply suitable averaging circuits. This way, however, would be both expensive and cumbersome. On the other hand, if in a system the output processes are always averaged, and we are interested in the resultant excitation states, then a number of elements working in an asynchronous way may be replaced by one element working on a higher frequency level.

We have made such a simplification also in our case and that is why the averaging (integrating) circuits are frequently used in our model. The electrical scheme of such a circuit is shown in Fig. 5; in the following

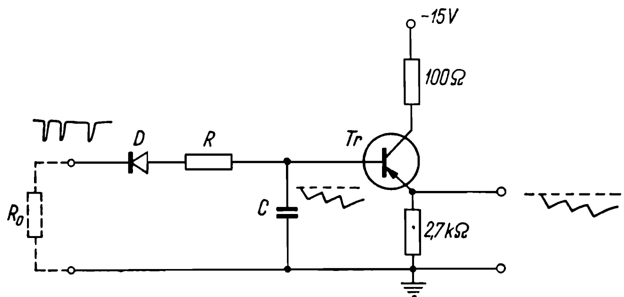

Fig. 5. Separating and integrating circuit. R_0, output resistance of the previous element; *D*, separating diode; *C*, integrating capacity; *Tr*, separating transistor. In the case of the application of positive pulses (inhibition) the diode *D* is inversly connected.

figures it is denoted with the sign of an integral. The diode *D* on the input of the circuit prevents discharging of the capacity *C* through output resistance R_o of the preceding elements, whereas the transistor Tr working in the common collector configuration prevents the backward influence of the next element upon the processes of the preceding elements.

Some properties of the modelled system have urged us to introduce another property to each element. As described in the first paper of this series, some inputs are not excitatory, but facilitatory; that is, they fail to activate the recipient centers but they increase their excitability. As a result the strength of excitation of a given element depends on the algebraic product of the signal applied to the facilitatory input and the sum of all other excitations.

The effect of such multiplication may be obtained with the help of the threshold characteristic, as it is shown in Fig. 6. The application of two small signals U_{i_1} and U_{i_2} (Fig. 6*b*) causes a signal U_{o_3} to appear on the output of the threshold element but none of those signals can excite separately the element. A small increase of the signals to the values U'_{i_1}

and U'_{i_2} (Fig. 6c) causes considerable increase at the output signal to the value U'_{o_3}. As we see, from Fig. 6*a*, the slope of the output to input characteristic (line 2) of the element (that is the increase of the resultant amplification) increases in this case considerably. As we see the threshold

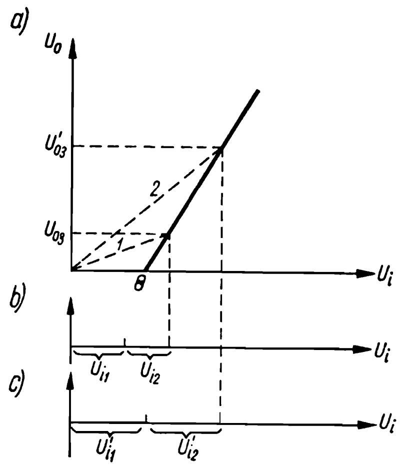

Fig. 6. Multiplication effect which appears in threshold element. *a*, Characteristic of the threshold element. 1 — resultant slope of the characteristic after the application of two small signals U_{i_1} and U_{i_2} as in Fig. 6*b*; 2 — resultant slope of characteristic after the application of two greater signals U'_{i_1} and U'_{i_2} as in Fig. 6c. *b*, The case of two small signals U_{i_1} and U_{i_2} which give together small surpassing of the threshold. *c*, The case of two greater signals U'_{i_1} and U'_{i_2} which give together greater surpassing of the threshold.

element may act as a multiplying element but only in a limited range of the input values. An improvement of the situation may be obtained by using several elements with different thresholds. It is possible that at

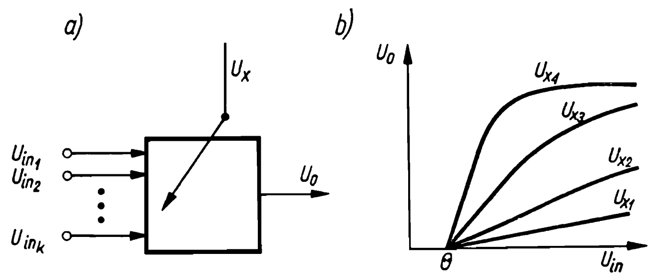

Fig. 7. Application of the multiplying input U_x which changes the slope of the characteristics. *a*, Designation of the multiplying element on block diagram. *b*, Characteristics of the element showing the dependence of the output signal U_o on input signal U_i for different values of U_x.

least a part of facilitatory effects appearing in the nervous system is caused by threshold properties of groups of neurons.

In our model it was often more useful to apply a special input which changed the slope of the characteristic of the element (that is its amplification) independently of the threshold properties. This is shown in Fig. 7 where U_{in} denotes the resultant additive excitation and U_x denotes the signal which changes the amplification of the element.

SOME REMARKS CONCERNING TECHNICAL ASPECTS OF MODELLING

The elements which were described in the preceding section may be set together in a system, the block diagram of which is presented in Fig. 8 and which was called Dewan. That system enables us to simulate a number of processes occurring in the alimentary system, provided that appropriate parameters of elements and values of connection weights (i.e. the values of couplings transmittances between centers) are set up.

The denotations given in Fig. 8 are in general the same as those in Fig. 3 of the preceding paper of this series (Konorski and Gawroński

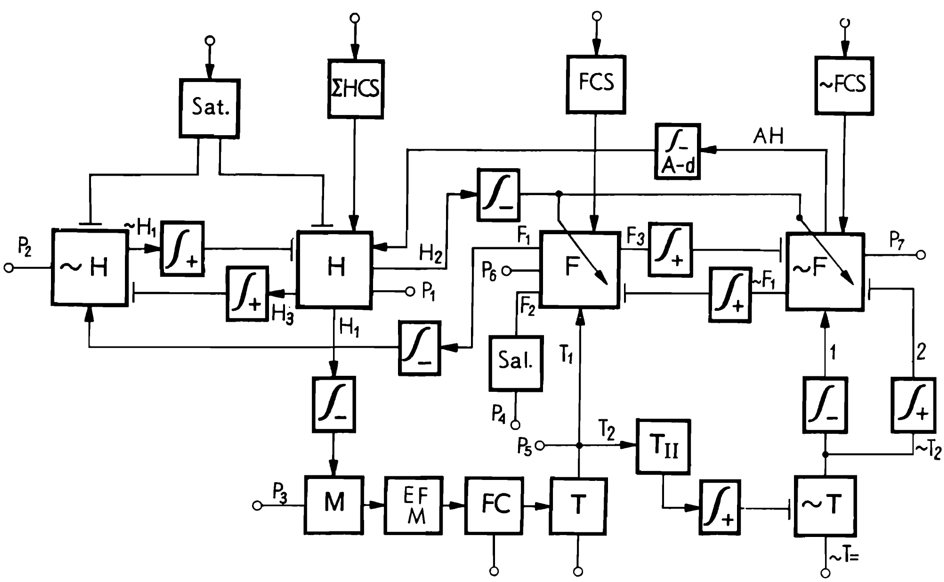

Fig. 8. The technical realization of block diagram of the arrangement modelling the essential processes in alimentary system. $\int_-$, averaging and separating elements which transmit excitatory signals (negative); $\int_+$, averaging and separating elements which transmit inhibiting signals (positive); $P_1 ... P_7$, the points of measuring instruments connection.

1970a). As it was stressed in the preceding section, the connections between particular centers are set up with help of the averaging-separating (integrating) circuits. Thus in the hunger system composed of two reciprocally interconnected neuronlike elements the hunger subcenter H transmits averaged inhibitory signals to the off-hunger subcenter ~H and vice versa. Hunger conditioned stimuli (HCSs) and levels of satiation (Sat), as well as other conditioned and unconditioned external stimuli, are simulated in our model with help of appriopriately regulated constant voltages.

The properties of the motor center M (see Konorski and Gawroński 1970b) are so chosen as to get single pulses simulating each instrumental response of the animal, when the pulse frequency from the hunger subcenter has a sufficient value. The connection between the motor effector M and taste receptor T denotes a purely causal bond and it is in operation only when the given instrumental movement causes presentation of food from a food container (FC). A special forming circuit T was applied in the model. In that circuit a pulse having trapezoidal form and the duration 1–3 sec is generated (Fig. 9) under the influence of every food

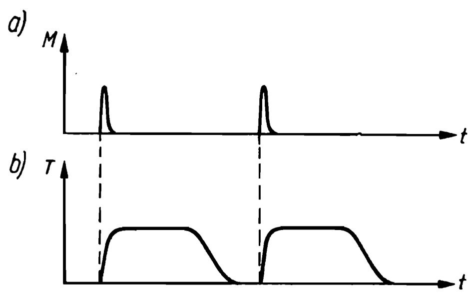

Fig. 9. The processes on the output of the taste center T (the figure *b*) under the influence of the activity of motor center M (the figure *a*) or of the unconditioned stimuli.

unconditioned stimulus (FUS). Since the excitation of the T receptor *ipso facto* precludes excitation of the ~T receptor we have applied in the model an additional element T_{II}, which under the influence of the FUS generates the inhibitory signals; these signals after being averaged inhibit the ~T receptor. The ~T receptor is permanently excited by external constant voltage $\sim T_{=}$.

Food subcenters (F and ~F) are reciprocally interconnected similarly as hunger subcenters. The amplitude of the signal from the T receptor reaching the F subcenter is so matched, as to get saturation level (upper bend of the characteristic from Fig. 3) at medium values of hunger, whereas the food conditioned stimulus (FCS) may be regulated over a broad range. The $\sim$T receptor excites the $\sim$F subcenter in a slightly different way: in the first period after the beginning of the excitation of the $\sim$T receptor intensive excitation of the $\sim$F-center through branch 1 takes place. After some seconds that excitation is partly compensated by the inhibiting signal transmitted through branch 2 from $\sim T_2$. In that branch an integrating circuit with a large time constant is employed, and for that reason the effect of inhibition appears after some delay. As was explained in the first paper, the H subcenter influences both antagonistic subcenters F and $\sim$F changing their excitability. Therefore the multiplying inputs denoted in Fig. 7 and 8 by inclined arrows going through the block as a sign of variable amplification, were used for that purpose.

Signals exciting the $\sim$H subcenter are transmitted from the F subcenter through typical integrating circuits. The same is true for the connection leading from $\sim$F to H.

There are three methods of measurement of the data obtained in experiments with Dewan. A very simple and demonstrative method consists in estimating excitatory processes in the centers by the intensity of light from small lamps placed in each element (excluding integrative circuits). For small frequences up to 10 pulses per second one can observe single flashes whereas for greater frequencies the intensity of light is an approximate measure of the degree of excitation. That method was used during the preliminary adjustment of the connection weights and thresholds of appropriate elements, as well as of the limits of the changes in the CSs.

More precise adjustment of parameter values was achieved by using a second method, consisting in frequency measurements of the elements with the help of a digital frequency-meter (Venner Electronics Frequency and Time Measuring Equipment Type Tsc 3336). This is the most accurate method of measurement which is reasonable in experiments with such models.

The third method of measurement consists in using fast pen-recorders connected with the outputs of appropriate elements. The connection points are denoted by P_1, P_2 ... P_7 in Fig. 8. For recordings, a 6-channel Philips-Osciloscript-PT2108 recorder was used. This recorder provided simultaneous recording of 6 pulse processes up to frequencies of about 300 c/sec. At higher frequencies the records of particular pulses merge in one curve owing to the inertia of the recorder pen and only approximate estimation of the frequency was possible on the basis of the degree of "smoothness" of the curve: the higher the pulse frequency, the more smooth is the record.

SOME REMARKS ON THE GENERAL PROPERTIES OF THE MODEL

Modelling of a system with the help of elements, and simulating the processes in particular elements and centers of that system, is often called structural modelling. As mentioned before, the main advantage of such modelling is the easiness with which the reading out of the data is accomplished and changes in the structure are introduced. This advantage was fully confirmed in the described model, but because of its relative complexity it had to be set in motion only gradually. A typical sequence of procedures was as follows.

1. Actuation of the food subsystem:

a) Preliminary setting up of the amplification of the F and ~F elements at values close to maximal. For that purpose the H_2 signal (Fig. 8) which plays the role of a multiplying signal is connected to the constant voltage source.

b) Setting up the couplings between F and ~F on the values previously selected (cf. Gawroński and Konorski 1970).

c) Setting up the amplification of the salivation center (Sal) on the values which correspond to a reasonable quantity of saliva drops at maximal excitation of the F subcenter.

d) Matching of the excitation of the ~F subcenter with help of the $\sim T_{=}$ signal.

e) Selection of the inhibitory connection weight from the TII center to the ~T center and the correction of the chosen value of $\sim T_{=}$.

f) Selection of the range of values of the FCSs in such a way as not to exceed in general the value of the FUS.

2. Actuation of the hunger subsystem and the connections between both subsystems:

a) Setting up of the ΣHCS at values permitting the full excitation of the H subcenter.

b) Matching of the weight of the connection from F to ~H center in such a way as to get excitation of the ~H subcenter close to maximum when the F subcenter is excited by the US.

c) Matching of mutual connection weights between H and ~H in such a way as to get considerable inhibition of the H subcenter when the ~H subcenter is activated by the FUS through the F subcenter, in spite of the action of ΣHCS.

d) Selection of the range of changes of the satiation center (Sat) in such a way as to get full inhibition of both subcenters, H and ~H, with full excitation of the satiation center.

e) Switching over of the multiplying signals from H to F and ~F (the connection H_2 — see point 1a) from the external voltage source to the H subcenter and adjustment of their value so as to get an appropriate interrelation between the F and ~F subcenters during the action of FUS and for the expected range of FCS changes.

f) Matching of the connection weight from the H subcenter to the M center at such a value as to get threshold excitation of the M center at some small value of excitation of the H subcenter, and to get maximal excitation of the H subcenter adjusted to maximal reasonable movement frequency simulated on the output of the M center.

As we see the adjusting procedure of the particular excitabilities and connection weights of the system is rather complicated and it is necessary to take into account all known neurophysiological data, otherwise it would be not possible to set up in a reasonable time such parameters which lead to reasonable results. It must be stressed that the above described procedure must be, as a rule, repeated several times because some signals, for example $\sim T_{=}$, ΣHCS or coupling H_2 from H on F and ~F strongly affects the state of the whole system, and may cause the necessity of changing some other parameters in order to get the proper relations between centers.

The accuracy of the measurements mainly depended on the stability and accuracy of standard elements as well as integrating elements, and this varied from 1% to 5% depending on parameter values. While this accuracy was not great, it was quite sufficient not only for qualitative appreciation, but also for approximate quantitative estimation and comparison with physiological experiments. Many results could be read out with an accuracy close to 1% and errors of about 5% appeared only in some cases when we worked close to unstable ranges of the processes, for example, close to the point of the switching over of the excitation from H to ~H or from F to ~F. As is the case when working with analogue computers, the most time consuming procedure was adjusting the parameters and choosing the couplings, whereas the measurements were much shorter, lasting not more than several minutes. It is important to note that in measurements of this kind there should be the participation of both a neurophysiologist who knows the results of analogous experiments on animals, and is able to choose properly the structure and the parameters of the elements and connections, and also a specialist of circuit theory and automatic control, who gives the interpretation of the phenomena and shows the possibilities and limitations of the investigated structure.

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