

# AUTOMATIC CONTROL IN BIOLOGICAL SYSTEMS

## CERTAIN HOMOGENEOUS NEURON NETS

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A mathematical model of a homogeneous nerve structure is considered. Its behavior is studied by means of computer simulation. It is determined how well its behavior can be predicted on the assumption that the system elements are continuously randomized.

In the investigation of neuron nets with random couplings the method of calculating them based on randomization of the elements, i.e., the assumption that the system elements are continuously rearranged at random, has been found to be very useful. An acquaintance with this method may be obtained from the work of L. I. Rozonoér [1] (for application to homogeneous networks see also [2]).

The present article contains a consideration of one class of neuron nets, connected with the study of the phenomenon of back inhibition. These nets are homogeneous, i.e., they have a regular geometrical structure. However, within certain limits the method of calculation based on randomization is applicable. For that region of parameters where this method is inapplicable, a second method of approximate calculation is exhibited, based on the study of stable configurations. We think that such configurations play an important role in the behavior of homogeneous nets. We also think that if there are no stable configurations, then the stimulation method gives a true qualitative picture of the behavior.

The phenomenon known in physiology as "back inhibition" was simulated by means of such homogeneous nets. This phenomenon was recently discovered at the output neurons of very many structures of the nervous systems of higher vertebrates (the hippocampus, the motor zone of the cortex, the olfactory system, the spinal cord, the cerebellum, etc.).

Usually the presence of back inhibition is proved by the following experiment. A certain group of output cells of the given nerve structure is excited antidromically (i.e., through the axones). Now at some of the output neurons a relatively prolonged inhibitory potential is observed. It is understood that the axones of the tested neurons are not stimulated. It is accepted that this result explains the existence of a special population of cells obtaining from the outputs an excitatory signal and, in turn, inhibiting the outputs, but no longer those or not only those which excite them. For the output cells of the spinal cord (motoneurons) such cells have been detected by direct histological investigation and have been named Renshaw cells.

Let us describe the general class of homogeneous neuron nets. For simplicity we shall limit ourselves to one-dimensional neuron nets with two types of neurons. This means that the neurons are arranged along two parallel straight lines (Fig. 1). For the models considered in the present article it is convenient to assume that the neurons of the first type are located at integer, the second type at half-integer points.

Each neuron may be found only in one of two states: excited, or "fired," and unexcited, or "extinguished." The time is discrete and the state of each neuron is a function of time.

The state of the entire system at the time  $t+1$  depends in a probabilistic manner on its state at time  $t$ , where the state of each neuron is defined by the states at the preceding time of only itself and its nearest neighbors. The homogeneity of the net means that the set of these neighbors and the dependence on them are the same for all neurons of the first type, and are the same for all neurons of the second type, to within a shift of the two lines.

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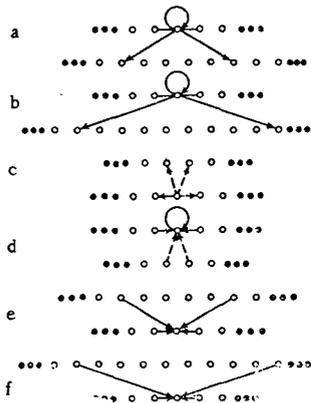


Fig. 1

The method of calculation based on randomization consists in randomly permuting all neurons of each type after each operating cycle. After randomization the events consisting in "firing" of neurons become independent and the operation of the system reduces to the iteration of pairs of numbers: the fraction of fired neurons of the first type and the fraction of fired neurons of the second type. It is interesting that such a coarse method can predict the correct qualitative pattern of behavior of the net (cf., [2]).

In all of our examples the neurons have simple back inhibition. In our case this means that the neurons of the first type excite the neurons of the second type, while the neurons of the second type inhibit the neurons of the first type. Further we shall call the neurons of the first type motoneurons and the neurons of the second type Renshaw cells. Of course these designations are exceedingly schematic, since the models are substantially simpler than real nerve structures.

In all examples, connections exist among the neurons, denoted in Fig. 1 by arrows. The full arrows show the excitatory connections, broken lines the inhibitory. At each integer time all excited neurons send out over the arrows emerging from them impulses which attain their destinations in identical standard time, less than unity. Each Renshaw cell (lower line) sends out inhibitory impulses to the two nearest motoneurons. Each motoneuron sends excitatory impulses to two Renshaw cells, not the nearest but more remote ones, at a distance  $n + \frac{1}{2}$ . In Fig. 1a,  $n = 2$ , in Fig. 1b,  $n = 4$ .

Thus in our models as in a real nerve system the Renshaw cell may inhibit a motoneuron which itself does not excite it. Below it will be shown that the value of  $n$  has a greater significance: the behaviors of the models for  $n = 2$  and  $n = 4$  differ substantially from each other.

Aside from this, simple excitatory couplings were constructed among neurons of each line: each Renshaw cell sends such impulses to the two neighboring Renshaw cells, and each motoneuron to the two adjacent ones and to itself.

In our models no signals other than those listed above are applied to the Renshaw cells (although in real nerve systems this is far from the case), and aside from those listed, there is one further input to each motoneuron. Over this input, after arrival of impulses from other neurons, an impulse is applied with probability  $\theta$  (completely randomly). Thus a random excitation is applied to the motoneuron defined by the number  $\theta$ .

As has already been stated, the system operates cyclically. At each integer time  $t$  all the excited neurons send out impulses over the connections emerging from them. After this the state of each neuron is recalculated according to the impulses which have just arrived at it. In different examples somewhat different rules of operation were used. Let  $k_t^+(A)$  and  $k_t^-(A)$  signify respectively the numbers of impulses sent to motoneuron  $A$  at the time  $t$ ;  $k_t^+(A)$  are excitatory (from the motoneurons),  $k_t^-(A)$  the inhibitory (from the Renshaw cells). Then after recalculation motoneuron  $A$  will be excited if  $k_t^+(A) - k_t^-(A) \geq 2$ .

We denote by  $l_t^+(B)$  and  $m_t^+(B)$  the numbers of impulses sent at time  $t$  to the Renshaw cell  $B$ :  $l_t^+(B)$  from motoneurons  $m_t^+(B)$  from Renshaw cells.

For such systems the question always arises: does the system conserve memory of its initial state after a sufficiently long time of functioning (is the system ergodic)? In certain examples which we have considered, ergodicity was absent, and two different operating regimes existed. It is interesting to note that the system properties differed for different values of the parameter  $\theta$ , characterizing the level of excitation arriving at the output cells. Namely, there existed a critical value  $\theta^*$  such that for  $\theta > \theta^*$  only one operating regime was possible, not depending (or almost not depending) on  $\theta$ , but strongly dependent on the geometry of the couplings among the neurons. For  $\theta < \theta^*$  this regime became unstable, and a second regime arose, strongly dependent on  $\theta$  and much more weakly on the geometrical couplings.

Strict proofs of ergodicity in the former and nonergodicity in the latter case exist only for sufficiently large and sufficiently small values of  $\theta$ .

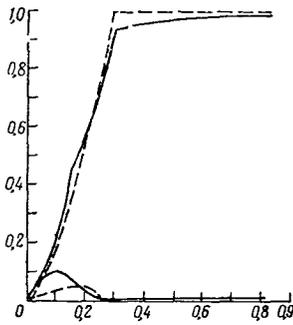


Fig. 2

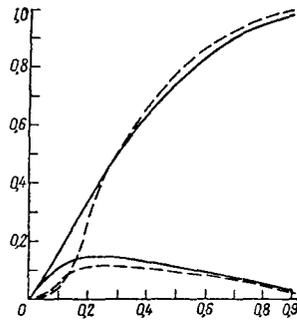


Fig. 3

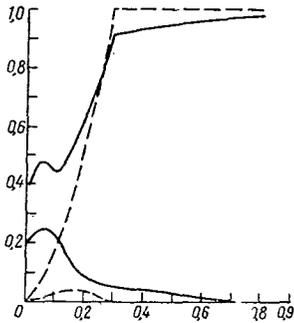


Fig. 4

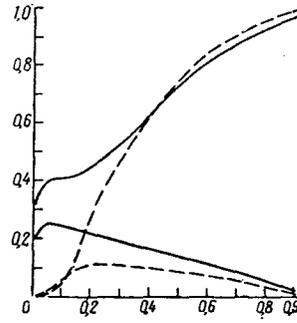


Fig. 5

After recalculation the Renshaw cell B will be excited if

$$\begin{aligned}
 & l_i^+(B) + m_i^+(B) \geq 2 \quad \text{in examples 1 and 3,} \\
 & \left. \begin{aligned}
 & l_i^+(B) + m_i^+(B) \geq 2 \\
 & l_i^+(B) \geq 1
 \end{aligned} \right\} \quad \text{in examples 2 and 4.}
 \end{aligned}$$

The operation of the net was simulated according to these rules. In the simulation the number of neurons was finite. Simulation was carried out with differing numbers of neurons to make certain that this did not influence the results.

Let us continue the description of the operation of the entire system. Immediately after recalculation the quantities  $d_1^+$  and  $d_2^+$  are calculated, denoting the ratio of excited motoneurons to their total number and the ratio of excited Renshaw cells to their total number. After these quantities are averaged with respect to  $d_1$  and  $d_2$  are obtained.

After this a random impulse arrives from outside with probability  $\theta$  at each motoneuron. A motoneuron receiving such an impulse is always excited, one not receiving it remains in the previous state. After this the next integer time  $t+1$  arrives and everything repeats from the beginning.

In all the simulation examples all neurons were at rest at  $t = 0$ .

We shall now describe the results of the simulation. The full line curves show the results of the simulation and the broken line curves the results of calculating such characteristics by the method based on randomization.

**Example 1.** Here  $n = 2$ . The system of couplings is shown in Fig. 1a, b, the results of simulation in Fig. 2. The quantity  $d_2^+(\theta)$  (broken line) is equal to zero for  $\theta \geq 0.3$ ; in the interval  $0 \leq \theta \leq 0.3$  it has a small maximum,

equal to about 0.04. The solid line curve has a maximum about 2.5 times as high, shifted to the left. This difference is apparently explained by the following. In our network the configuration of two adjacent motoneurons does not extinguish in the absence of external influence, in contradistinction to configurations of two nonadjacent motoneurons. The method of randomization does not take into account the difference between configurations of adjacent and nonadjacent motoneurons. The fact that the maximum is shifted to the left is apparently explained by the following. If two adjacent motoneurons are fired, there is a high probability that the Renshaw cell receiving couplings from the fired motoneurons will also fire. In this situation, if some motoneuron adjacent to the given pair fires, a further Renshaw cell immediately triggers, which extinguishes one of the fired motoneurons; at the same instant the fired motoneuron itself extinguishes from the previously fired Renshaw cells.

For the broken line curve  $d_1(\theta)$  the steep rise to 1 in the region  $0 < \theta \leq 0.3$  is characteristic. Here, perhaps, the close agreement between the calculated and experimental curve is most remarkable.

**Example 2.** The conditions of this example differ from those of example 1 only in the conditions for triggering the Renshaw cells. Concretely, the condition  $I_1^+(B) \geq 1$  is added, i.e., that among the impulses arriving at the Renshaw cell there be at least one from above. The full and broken line curves are here very similar (Fig. 3). A small qualitative difference exists only for small  $\theta$ . A very important feature of this example, distinguishing it from example 1, is that  $d_1(\theta) > 0$  and  $d_2(\theta) < 1$  for all  $\theta$ .

This is connected with the fact that here the Renshaw cells are not in the state of maintaining themselves without fired motoneurons. It can be rigorously justified if we assume the existence of  $d_1(\theta)$  and  $d_2(\theta)$  themselves.

In contradistinction to example 1,  $d_2(\theta)$  grows much less steeply,  $d_1(\theta)$  begins to decrease later and decreases more slowly. The fact that  $d_1(\theta) > 0$ ,  $d_2(\theta) < 1$  shows that in the given net its state is defined by the prehistory only for a short time.

**Example 3.** The conditions are the same as in example 1, but  $n = 4$  (cf., Fig. 1b). The broken line curves coincide identically with those of example 1. The basic difference of the experimental curves from the analogous curves of example 1 is that  $d_1(\theta)$  and  $d_2(\theta)$  do not tend to zero as  $\theta \rightarrow 0$  (cf., Fig. 4). Thus the method of calculation based on randomization does not give here a correct picture which, evidently, is connected with the following circumstance. In this case there exist groups of motoneurons which, being fired and protected from external excitation, maintain themselves. More exactly, this signifies that for  $\theta = 0$  these groups, once fired, never extinguish. These are, for example, groups of  $l$  adjacent motoneurons for  $2 \leq l \leq 10$ . But in Example 1 there also exist self-maintaining groups of motoneurons: groups of  $l$  adjacent for  $2 \leq l \leq 6$ .

In order to comprehend the different results, it is necessary to investigate the stability of these groups for small, but nonzero values of  $\theta$ , specifically it is necessary to compare the probability of formation of such groups and their mean lifetimes, defined by the probability of perishing. In discussing example 1 it was pointed out that a group of two fired motoneurons could die out. For this it is first necessary that a Renshaw cell to which there is a connection from one of these motoneurons fires. The probability of this event is of order  $\theta$ , since for this it is sufficient that the motoneuron sending the second impulse to this Renshaw cell fire for one clock time. Once fired, this Renshaw cell extinguishes in the next clock time, but must fire the adjacent cell to which there is a coupling from the second motoneuron of our pair; this again fires the first, etc. For a time of the order of  $1/\theta$  they will both continue to fire. Thus only during a time of order of magnitude not greater than  $1/\theta$  will a pair of fired motoneurons not fire any Renshaw cell. During a further time of the order of  $1/\theta$  a motoneuron adjacent to the fired pair will fire, and when it does the pair will perish as described above.

We now remark that a single fired motoneuron extinguishes. Therefore the probability that a fired pair appear is of the order of  $\theta^2$ . A comparison of these estimates elucidates why the fraction of fired pairs in example 1 tends to zero as  $\theta \rightarrow 0$ . For groups of a larger number of fired neurons the lifetime and probability of appearance is still smaller.

The same considerations literally apply to example 2.

Let us now consider example 3. Let some pair of adjacent motoneurons fire. During a time of the order of  $1/\theta$  the Renshaw cells which receive couplings from this group begin to fire. The time elapsed during which they all fire is also of the order of  $1/\theta$ . Assume that they are all fired. But the motoneurons to which they send inhibitory couplings are far from our pair, and if along with them a motoneuron fires, it itself is not extinguished, and the pair does not extinguish; the triplet obtained will be stable for a time of the order of  $1/\theta$ .

In exactly the same way, groups of 3, 4, 5 neurons will pass into groups of 4, 5, 6, where only groups of 6 neurons will be unstable, passing in a time of the order of  $1/\theta$  into groups of 4 neurons.

For double excitations, which happen with probability of the order of  $\theta^2$ , groups of 2, 3, 4, 5 neurons pass into groups of 4, 5, 6, 7, of which the groups of 6 and 7 neurons are unstable, and pass into groups of 4 and 3.

Thus groups of 2, 3, 4, 5 neurons, passing into each other, have lifetimes of the order of  $1/\theta^3$ , since only simultaneously excited triplets of adjacent neurons can bring them to perish. If it be taken into account that the probability of appearance of pairs of fired neurons is  $\theta^2$ , it becomes clear why in this example  $d_1$  does not tend to zero as  $\theta \rightarrow 0$ .

The approximate method giving the broken line curves does not capture this phenomenon, since it permutes the neurons after each cycle and breaks up the groups of fired neurons.

It is understood that considerations of the type just presented are not a strict mathematical proof, although the method of randomization also is not. Therefore complete assurance that even they give in all cases a true qualitative result is lacking. It appears to us that it would be interesting to investigate the region of their applicability.

Example 4. In this example the condition for firing of a Renshaw cell is the same as in example 2, but  $n = 4$ . For small  $\theta$  the graph of this example is similar to that for example 3, and for large  $\theta$ , to the graph of example 2 (Fig. 5). The lifetime estimates for self-maintenance of neuron groups proposed for example 3 literally apply to this example also. The inequalities  $d_1(\theta) > 0$  and  $d_2(\theta) < 1$  for all  $\theta$  can also be proved if we assume the existence of  $d_1$  and  $d_2$ . This example conserves the correctness of the previous conclusions.

Substantially less steep than in example 3, the drop of  $d_1$  after the maximum is explained by the slower growth of  $d_2$ .

#### LITERATURE CITED

1. L. I. Rozonoér, "On random logic nets," *Avtomat. i Telemekhan.*, Nos. 5, 6 (1969).
2. O. N. Stavskaya and L. I. Pyatetskii-Shapiro, "Homogeneous nets of formal neurons with spontaneous activity," *Problems of Cybernetics [in Russian]*, 20 (1968).