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DISCUSSION

We have three people who are going to take up the problem from where it was left before coffee break. The first is Dr. Derksen, who is here at Leiden in the Physiological Laboratory and I understand that he is an excellent home-grown model-maker.

DERKSEN: Mr. Chairman, Ladies and Gentlemen, I will talk this morning about the same kind of models my friend Leon Harmon presented to you last Wednesday morning. I think he deserves much credit for having pioneered the revival of the analog approach. And I must say I was rather happy to find his first announcement in Science two years ago. We here in Leyden had been developing a neuron analog, an electronic circuit simulating a neuron as it manifests itself to the electrophysiologist. We really didn't know why we started it. Sometimes it seemed difficult to justify the time and money spent on it. Then it is always a good thing to hear that there are other people moving in the same direction.

A large part of the discussion going on at this Symposium, especially between neurophysiologists and let us say model makers sounded quite familiar to me already. I am working as a physicist among a number of physiologists here in the physiological lab. And that means that in the beginning there were difficulties in understanding each other and in appreciating each other's methods and ways of thinking. As far as I can see workers in the field of neuron analogs or membrane models have the difficult job of being "trait d'union" between neurophysiologists on the one hand and experts in automata theory and modern mathematics on the other.

The applicability of the electronic neuron analog in model studies is, I think, restricted to networks which in essence can be simplified to a few hundred cells. The network must have a single function or purpose. Preferably, it must not be adapting or learning. I must admit that I am a little bit shy about so-called higher functions of the nervous system, I am rather more attracted to peripheral systems. Sometimes, I assure you, I'd like to go more and more peripheral, passing the skin of the organism and go back again to experimental physics. But even in this one has been preceded by Helmholtz.

The use of working models in biology and physiology is quite common. Different kinds of models have been constructed and studied for muscle fiber, heart fibers and axons. Making a neuron model is much more difficult than simulating an axon. Dr. W. K. Taylor of University College in London and Harmon of the Bell Telephone Labs. were as far as I know the first to come out in the open with the fruits of their efforts. And I am convinced that from this sector in model making a number of significant contributions to neurophysiological thinking will be made in the near future. Two factors have been mainly responsible for this new development.

First, in the years since 1950 a mass of data on the functioning of neurons became available as a consequence of the introduction of single unit extra- and intracellular recording by means of microelectrodes.

Secondly the successful development and application of general purpose electronic analog computers, also since-roughly-1950. This type of computer is certainly more restricted in its field of application than the digital computer. But it offers a number of important advantages in such fields as solving systems of non-linear ordinary differential equations. High computing speed, accessibility of all variables, ease of changing parameters and simple programming are the most important advantages.

Probably you will know that the dependent variables in a problem programmed on an analog computer are represented by voltages or currents proportional to these variables and interacting in the same way. Parameters are represented by coefficient potentiometers, by resistors or by capacitors. Time is generally the independent variable. This means that the general purpose analog computer would be an excellent tool for solving the Hodgkin-Huxley equations for squid giant axon membrane in a variety of different situations. Important work on this subject has in effect been done by Dr. R. Fitzhugh during the last few years. But even in those cases where experimental findings have not or not yet been boiled down to descriptive empirical equations, an experienced programmer can often make a very good guess directly from oscilloscope pictures, graphical representations and numerical data.

Consequently one could ask oneself whether it is possible to combine the many observations on a certain type of neuron or homogeneous class of neurons in an analog computer programme. Things like amount of transmitter substance and its postsynaptic effects, membrane voltage at the firing site and level of threshold would be represented by time-dependent voltages in an electrical network. Phenomena such as synaptic facilitation, lag and attenuation due to propagation along dendrites, accommodation and refractoriness should be found back when the programme is running. Of course nobody would use an expensive general purpose computer for simulating a neuron, prototype development excepted.

Because the goal is to study assemblies of interconnected neurons it is necessary to develop a small specialised electronic circuit which is not too expensive. Unfortunately our knowledge about neurons still shows many gaps and contradictions, despite the enormous efforts of the last fifteen years. A really clear, consistent and complete picture of the sequence of phenomena between the arrival of a presynaptic volley and the firing of the neuron and its after-effects cannot be given yet. The work of Eccles and his collaborators on the cat's motoneurons comes quite near to it. The motoneuron is a rather special kind of cell however and it does not belong to a system which is typically data processing in the sense of this Symposium's title.

Even classical properties such as the course of excitability of the neuron's firing locus seem to need further research and discussion. This I would illustrate by citing a remark made by Fuortes in a recent issue of the *Journal of General Physiology*. "It would be desirable", says he, "to specify what is meant by refractoriness and by accommodation besides stating that the first is an unknown process brought about by firing and the second is an equally unknown process due to the stimulus".

This remark, at the end of a careful analysis of existing data, made me rather happy I must say. I had just read all the literature on this subject over and over and got the impression that nobody here saw any problem at all.

Another difficulty in gathering facts together is in terminology. For an example, I will cite Dudel and Kuffler. They say: "The term facilitation frequently covers a variety of processes which lead to an increased response, including temporal and spatial summation, recruitment, or removal of inhibition. A more restricted definition will be used here; we shall speak of `facilitation' if a nerve impulse in a presynaptic fibre sets up an increased post-synaptic potential due to preceding impulses in the same nerve fibre".

Finally a fundamental difficulty is inherent in our main source of knowledge on the dynamical properties of the neuron, the method of intracellular recording by means of micropipettes. Everything that happens on a closed membrane surface of very complicated shape and with physicochemical properties varying spatially and temporally results in the single physical scalar of a time dependent voltage somewhere in the cell body. Very puzzling experimental results could perhaps become more readily understandable if we would experimentally resolve their spatial components.

This is generally not possible. An exception is given by Tauc's studies on Aplysia giant neurons. But illustrative as the giant nerve, synapse or neuron may be, they are rather special cases.

What we have said is nothing new. It is certainly not intended as a criticism nor does it come as a consequence of a fundamental pessimism in regard to the solvability of neurophysiological problems. What I should like to point out is that the present state of factual knowledge leaves the model designer rather much room for ambiguity. He is often forced to fill up gaps in the data with guesses. One of the consequences is that existing neuron models like those of Harmon, Jenik and others and the one I worked out here in Leyden all show, together with common aspects, a number of differences. Permit me to tell you a few particulars on my own approach. My goal has been to simulate not only the neural transfer function but also to reproduce the waveforms of membrane potential as found in intracellular recordings. Despite difficulties that sometimes arise in interpreting the results, a large amount of direct information about events in nerve cells stems from these recordings and from experiments with intracellular electrical stimulation. In order to facilitate comparison with experiment and to limit in this way the large number of alternative solutions we decided to provide our black box with a terminal giving the same kind of inside information as a microelectrode in a real nerve cell.

These requirements finally led to a circuit having the well-known RC-combination as its nucleus, shunted by a time dependent, voltage stable negative resistance. This type of negative resistance once was a rather rare thing in electronics. It is now found in the stationary characteristics of the tunnel diode. Nerve axon shows this characteristic but only as a dynamical, time dependent phenomenon. In our model we synthetised it by

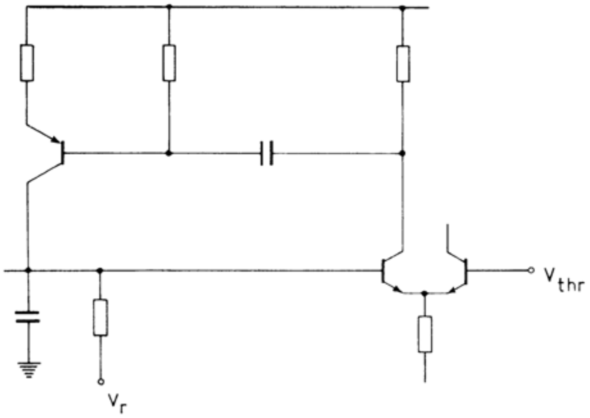

Fig. 1. Negative resistance circuit used in neuron analog.

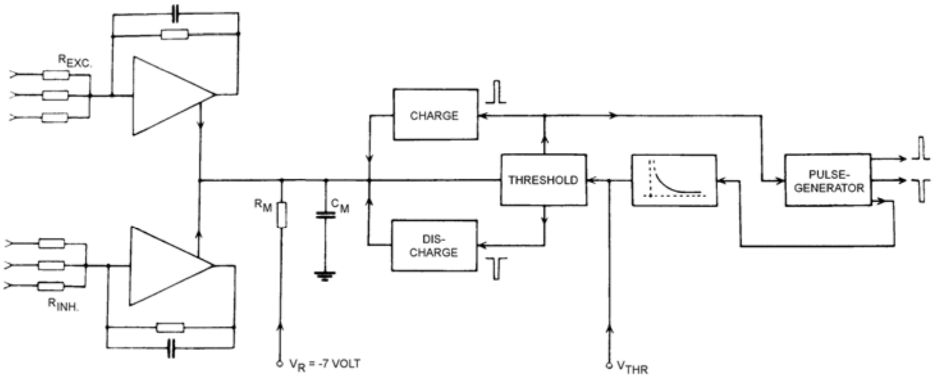

Fig. 2. Block diagram of neuron analog.

means of complementary transistors. Figure 1 shows, very much simplified, the type of circuit used for changing the membrane analog when threshold is exceeded. The next figure gives the block diagram of the analog. One sees that the basic circuit has been completed by a membrane discharging circuit representing potassium outflow. Further details have been presented elsewhere in this Congress by my colleague Van der Mark.

The approach I just sketched divides the neuron into two functional parts. The first is the sequence of processes between presynaptic action potentials to the postsynaptic potentials as measured in the cell body. That means that the time courses and magnitudes of the psp's after a single volley as well as with repetitive excitation must be reproduced faithfully. The second part concerns the firing characteristics of the cell, the time course of the action potential with its after-potentials, refractoriness and accommodation. I dare say that we have come fairly close to the goals we set ourselves. To give a few examples: Figures 3 and 4 show the model programmed as a motoneuron, figure 5 shows the type of firing found in Renshaw cells. Simulating all these waveforms by means of electronic circuit components is often like fitting square pegs in round holes. Our circuitry is mainly based on complementary transistors. But we have very often felt

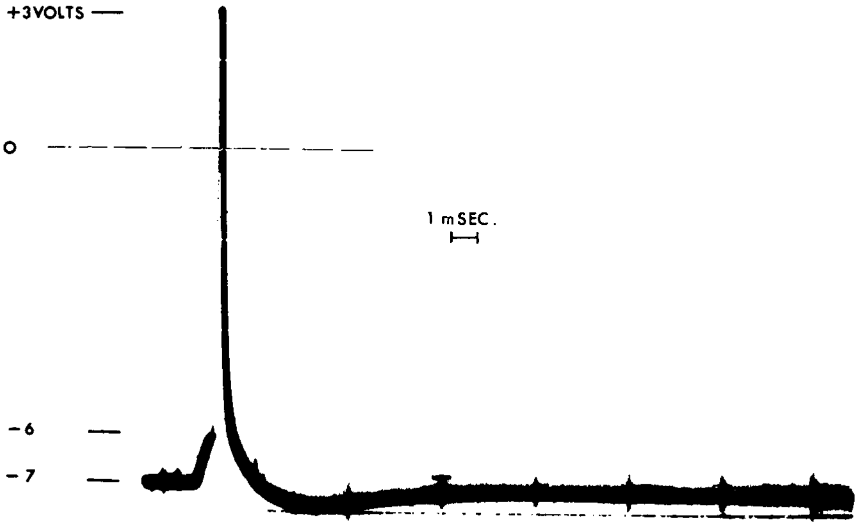

Fig. 3. Action potential of motoneuron model.

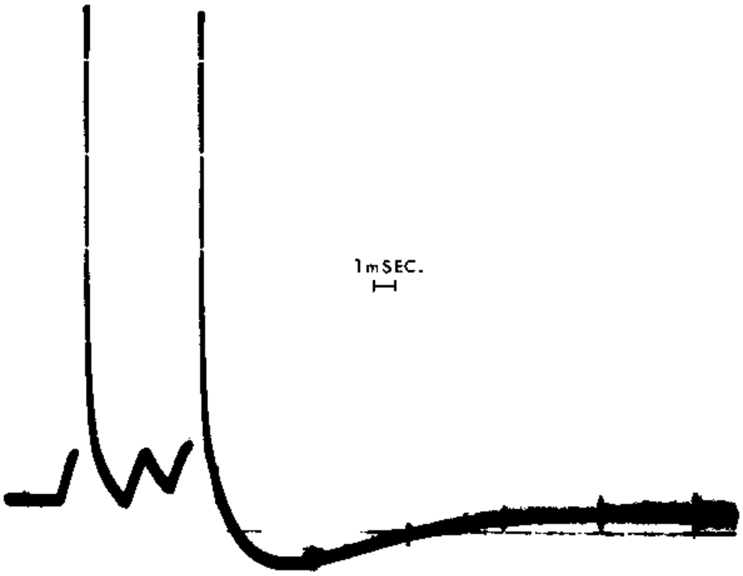

Fig. 4. Action potentials of motoneuron model. Refractoriness.

a need for two circuit elements, which unfortunately do not exist in a compact and inexpensive form. The first is a resistor with an S-shaped current-voltage characteristic, the second is a resistance controlled by an external voltage.

Of course considerations of price, compactness, reproducibility and stability resulted in additional restraints on our design. One short remark on stability. Resting membrane voltage is minus seven volts in our model, threshold generally is half a volt more positive. Drift, hum and noise of both these levels remain within two millivolts.

Designing a special purpose analog computer around these analogs presents a number of problems. We have planned for one hundred neuron analogs. There had to be

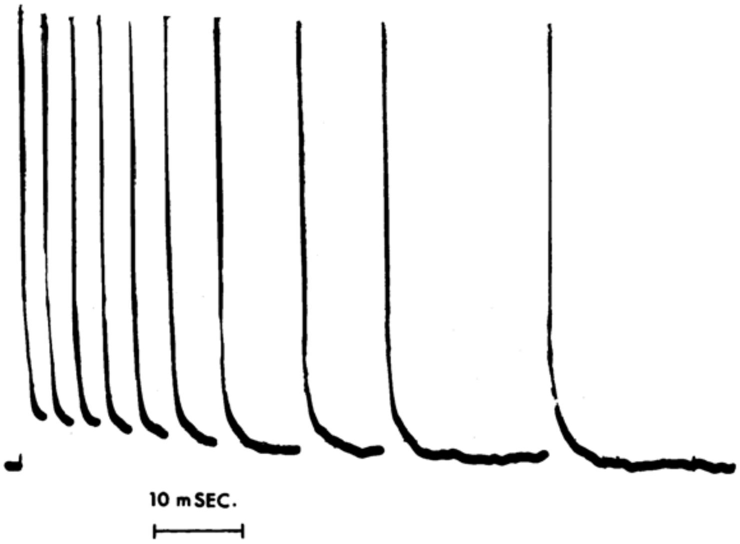

Fig. 5. Burstwise firing as found with Renshaw-cells.

facilities for quickly testing them. Freedom from unwanted interactions is essential. We had to design a noise generator having a large number of uncorrelated outputs. In order to reproduce spatio-temporal pulse patterns we built a kind of artificial Limulus eye, without lateral inhibition however. If we use photoresistors as interconnection resistances it is possible to explore a great number of interconnection patterns by illuminating through different masks and varying overall light intensity.

Network activity is studied by means of stroboscopic visual read out. Our method of studying model networks strongly resembles the Lettvin-Maturana approach of exploring the behaviour of retina and tectum of the frog. We can change the network configurations however.

All I've said up till now leads to the question of the use and applications of these models, imperfect though they may be at the present time. The answer is straightforward in principle. If one has at his disposal a calculus or a computer, it is possible to draw far more conclusions from experimental fact than is possible by verbal reasoning. The calculus could be a graphical method, it could be based on symbolic logic or it could be based on classical mathematics. The computer could be digital or analog. How it is done is irrelevant but the neurophysiologist rightly demands that the initial assumption concerning the neuron's behaviour be not curtailed too heavily. This is unfortunately the case with the Rashevsky-Landahl and the McCulloch-Pitts approaches of the 1940-1950 era. But in those cases where it has really been possible to start from an adequate mathematical skeleton of neuronal behaviour and to derive the mode of functioning of a certain neural network, such analysis has had a great impact on neurophysiological thinking. There are two examples.

The first is Beurle's analysis of wave propagation in cell masses and the second is Reichardt's analysis of lateral inhibition. Both gentlemen are participants in this Symposium, so there is no need to go into details. The formal-mathematical approach is unfortunately restricted in its applicability, especially where nonlinear processes are involved. Everybody who has worked out a number of solutions of some nonlinear differential equations on a computer will have been impressed by the completely unforeseeable variety of these solutions for minor changes in parameters and initial conditions. And there is no hope of seeing solutions in a reasonable time without use of a computer! Numerical solutions take lots of time to obtain and we are lazy people.

Now the electronic neuron analog is a highly specialised, real-time analog computer. One can program it in order to simulate different types of neurons by means of small variations in circuitry. Numbers of analogs can be combined into neural networks using histological data as far as these are available. The transformation of spatiotemporal input patterns can be studied and recorded often in ways that are impossible to realize in animal experimentation. All this must lead to new experimental approaches, otherwise it has failed.

Besides the applications already mentioned by Harmon last Wednesday, I should like to indicate, without attempting to be complete, some others which could be interesting to pursue.

1. Cell arrays with lateral interaction

Reichardt's algebraic analysis of lateral inhibition is valid for the steady state of the generator potentials of Limulus eccentric cells. It could be extended to the full time course of these potentials. Transient generator potentials and burstwise firing are certainly more pertinent to visual perception in vertebrates than repetitive firing at nearly constant frequencies. Repetition of the pattern of neural interaction leads to Fessard's picture of regularly interwoven and repeated connection patterns.

2. The microstructure of action potential trains

It has been mentioned a few times in the course of this Symposium, that it would be of practical interest to have an idea on what constitutes a difference between two input pulse trains for a neuron. The criterion is the kind of pulse train produced by the neuron itself and the course of excitability that follows it. A lot of smoothing occurs because of temporal summation and different time constants play a role here, such as those of descent of psp, membrane impedance, refractoriness and so on. It is possible that bursts of pulses of high frequency can be simply represented by a single number whether they are regularly spaced or not. The problem is very suitable for exploration by means of neuron analogs.

3. Neuromuscular servoloops

This is a very vast subject covering an enormous amount of neurophysiology since Sherrington's time. Although the receptors, neurons, and effectors of the motor system are perhaps the best known in neurophysiology it is a tremendous task to reconstitute their interactions in a model system. Parts of it could be done however. It is a remarkable thing that work done in Granit's laboratory (see his lecture at this Congress) brings us again to lateral inhibition.

4. The auditory system

Harmon mentioned already the spiral innervation of the cochlea. Further, Allanson and Whitfield's views on the structure of the cochlear nucleus, presented at the Third London Symposium on Information Theory (1956) offer a number of opportunities for model studies. Most of it, this will surprise nobody, comes very near again to lateral inhibition.

5. Data-processing in the frog's visual system

Lettvin and Maturana's work has revealed the existence of two classes of peripheral neurons functioning as detectors of moving contours and moving small objects. The work of my colleague J. J. Schipperheyn on the same system, done with the utmost care, proves that these neurons are indeed retinal neurons. However this is irrelevant in so far that a really very concrete case of peripheral data processing or filtering is performed. It is possible to invent a number of neuronal networks doing the same job of moving target indication. Working closely together with neurophysiological experimentation the model maker could step by step reduce the number of alternatives, and finally arrive at the most probable network configuration. All this takes a lot of time of course, but it is likely to be very rewarding.

6. Membrane and threshold fluctuations in peripheral axons

My compatriot Verveen has pursued Pecher's research on fluctuations in excitability in peripheral nerve, such as frog sciatic, crab and squid nerves. His findings have led to a series of model studies by Ten Hoopen and Den Hartog who use Harmon's analog in a modified version. Threshold fluctuations in a nerve section are practically impossible to evaluate mathematically. Already the model studies, which will be published next year, have initiated a number of experimental investigations.

7. Spontaneous activity

It seems to me that this phenomenon is drawing much attention during the last few years, and I should like to make a few comments on it. The increase of interest in spontaneous activity is perhaps caused by the circumstance that it is so much easier to analyze the statistical properties of random firing, since digital computers or pulse interval analyzers are more readily at hand. Important results have already been published by P. 0. Bishop and collaborators, by Grossman and Viernstein and notably by Gerstein and Kiang from Rosenblith's laboratory at MIT. Here of course one would try to find a model having as its main ingredients a membrane circuit and membrane threshold levels, one or both fluctuating. This model should reproduce the pulse interval histograms and the poststimulus histograms as derived from experimental data. Depending on the complexity of the initial assumptions, the model's behaviour can be derived by means of pencil and paper mathematics alone or by computer studies. Here I think neuron analogs are extremely useful. In combination with noise generators and pulse interval sorting equipment a large number of hypotheses can be evaluated in a short time. Moreover only one or at most a few neuron analogs are needed unless one wants to study a randomly firing neuron as an element in a randomly active network, as has been done by Farley on a digital computer. The phenomenon of spontaneous activity has been mentioned several times during the Symposium. I hope it will be thoroughly discussed this morning or in the final session.

Now it does not matter what term you prefer for the irregular firing of nerve cells in the absence of sensory input, but don't call it noise. I fear this would lead our thinking in the wrong direction of amplifier noise, noisy transmission channels and so on. A large number of different nerve cells in different animals do not fire spontaneously. And there is no reason to suppose that ganglion cells in the cat's retina for example, are of lesser quality-more noisy-than those of the frog. As long as it is not fully clear what the neural signal is, spontaneous activity shouldn't be called noise. It could for example constitute a reference level or it could signal the general state of other parts of the CNS. I heard so many possible significances attributed to spontaneous activity that it will surely be necessary to do a lot of experimental work and model studies in order to make a choice. If we apply the conventional concepts of membrane potential and. threshold, then spontaneous activity can only be caused by fluctuations in one or both of them. Membrane potential fluctuations can have their origin in thermal noise or they can be caused by random synaptic bombardment. And as far as estimates of these fluctuations exist they lead to the conclusion that the mean values of membrane potential and threshold must lie quite near to each other. Certainly much closer than the ten to twenty millivolts reported for quiet neurons and axons. But in view of the surprising constancy of the statistics of the interval distributions one should expect these levels to be regulated by controlling influences having long time constants, time constants of the same order as shown by post-tetanic potentiation and by accommodation. It wouldn't be surprised if these controlling influences were found to be exerted by satellite cells. But regulation implies that the neuron would not be capable of following high frequency excitation for a very long time and signaling would have to be done in short high frequency bursts. This reminds the physicist or engineer of an a.c. amplifier with negative feedback through a low pass filter instead of the usual high pass filter in the input lead (fig. 6). The difference is that the neuron reacts to varying presynaptic-pulse intervals whereas the amplifier reacts to smoothly varying voltages

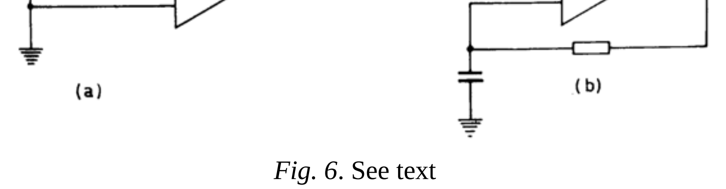

Fig. 6. See text

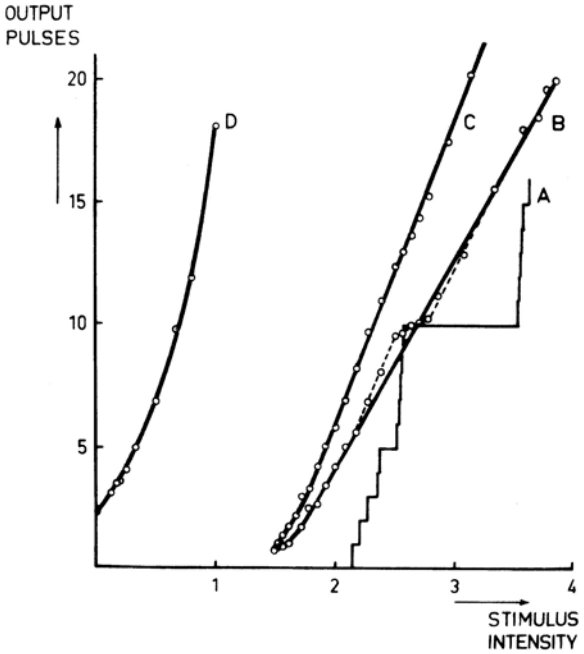

Fig. 7. Model programmed as in fig. 4. Curve A: input 10 pulses, width one millisecond, interval 10 msec. Curve B: same input, noise added. Curve C: continuous excitation. Curve D: as B, threshold lowered.

Abscissa: intensity of excitation, linear scale in relative units. Ordinate: number of action potentials produced by model in 130 msec. interval. This interval starts when the first excitatory pulse arrives in cases A. B and D.

What I am suggesting now is a rather wild guess of course. But it can be pursued to its logical consequences and these can be checked against past or future experiments. Let me present here a first crude approach. We supplied a neuron analog with bursts of ten pulses spaced by equal intervals of ten milliseconds. The intensity of the pulses was varied and we counted the number of action potentials produced by the analog. Fig. 7 curve A shows the result. Threshold was 0.6 volt above the resting membrane voltage. This would be 6 millivolts in a real neuron. Curve B shows the same relationship when membrane voltage fluctuations of 70 microvolts r.m.s. were added.

This results in a continuous curve. Curve D gives the same case, except that threshold was 0.06 volt (0.6 millivolt in real cells) which resulted in spontaneous activity with a mean rate of 20 pulses per second. You see that curves B and D are rather similar, except that in case D the model is able to react to much weaker inputs.

There are situations where this mode of functioning might be biologically useful, such as detection of very low intensity sensory inputs. Generally, a sensory input is converted into a generator potential which causes a train of impulses. The first conversion shows no threshold as far as I know. But the second one generally does, so that sub-rheobase generator potentials would get lost. If we suppose the threshold of the first pulse generating cells to be very low however even the smallest generator potentials would result in small changes in pulse density. Detection now necessitates averaging over very many channels. Fortunately these are present in complex sensory systems. Ideas of this kind have been suggested by Pumphrey (1950), Roeder (1955) and Ruck (1961). Closely related are remarks on the cochlea made by Tasaki (1960).

Curiously enough the use of so called D.C. superregenerators as simple high sensitivity signal detectors has recently been suggested in a purely technical context. This type of circuit comes very close to a neuron constantly flaring up into an action potential, starting from noise or from signal plus noise in such a way that pulse intervals increase monotonically with initial level. In technology it seems to be a pressing problem. Mosaic detectors need a multiplicity of expensive amplifiers. The solution should be to construct a mosaic of these superregenerators, which solves at the same time the problem of telemetry. These parallel structures, rather new and difficult for the engineer are very familiar to the biologist, who doesn't have to build them however.

The problem of spontaneous activity which I have elaborated somewhat is of course only one of the many points where neural analog hardware can be useful as an aid in reasoning about neurophysiological phenomena. It must be stressed however that it is an aid and nothing more. And it must be stressed also that a very close collaboration between the neurophysiologist and the model maker is necessary in order to get good results. This approach in modeling is much more concerned with actual physiological detail and mechanism than-let us say-the mathematical or system-engineering one. Very often my kind of people have to look at both sides, are asked to translate back and forth between experimental neurophysiology and modern applied mathematics. If the opportunity is given to us, I think we could make some useful contributions. What Harmon and I told you in this symposium and what we and other people in this field have published is not much more than a first announcement. Most of our efforts have been spent on developing a satisfactory prototype, measuring properties of the single unit, changing it again and again, and on developing a workable computer system with these things. And, to end this talk, we need still more data and we need some time. For as an object of scientific research the nervous system is extremely tough.

REFERENCES

ALLANSON, J. T., and WHITFIELD, I. C.: The cochlear nucleus and its relation to theories of hearing. *Information. Theory,* Third London Symposium, C. Cherry, ed., Butterworth, London 1956.

BEURLE, R. L.: Properties of a mass of cells capable of regenerating pulses. *Philosoph. Trans. Royal Soc. London,* series B, 240, 55-94, 1956.

BURGESS, J. Q.: New concepts in detecting weak electromagnetic signals. *Electronics*, 34, 49-55, 1961

DERKSEN, H. E., and MARK, F. VAN DER: Influence of resting activity of sensory cells on sensory threshold. *Proc. XXII Int. Congr. Phys. Sc.,* vol. II, p. 950, Excerpta Medica Foundation, Amsterdam-New York 1962.

DERKSEN, H. E.: A neuron analog simulating the electrical properties of the cat's motoneurons,
Acta Physiol. Pharmacol. Neerl., 10, 164-180, 1961.

DUDEL, J., and KUFFLER, S. W.: Mechanism of facilitation at the crayfish neuromuscular
junction. *J. Physiol.*, 155, 530-542, 1961.

FARLEY, B. G.: Some results of computer simulation of neuron-like nets. *Fed. Proc.,* 21, 92-96, 1962.

FARLEY, B. G., and CLARK, W. A.: Activity in networks of neuron-like elements. *Proc. 4th London symp. Information Theory.* Butterworth, London 1960.

FESSARD, A.: The role of neuronal networks in sensory communication within the brain. 1959. In: *Sensory Communication,* 585-606, W. A. Rosenblith ed. M.I.T. Press and J. Wiley, New York, 1961.

FUORTEs, M. G. F., and MANTEGAZZINI, F.: Interpretation of the repetitive firing of nerve cells. *J. Gen. Phys.,* 45, 1163-1179, 1962.

GERSTEIN, G. L., and KIANG, N. Y.-S.: An approach to the quantitative analysis of electrophysiological data from single neurons. *Biophys. J.*, 1, 15-28, 1960.

GROSSMAN, R. G., and VIERNSTEIN, L. J.: Discharge patterns of neurons in cochlear nucleus.*Science,* 134, 99-101, 1961.

HARMON, L. D.: Neuron model. *Science*, 129, 962, 1959.

HARMON, L. D.: Studies with artificial neurons. *I. Kybernetik*, 1/3, 89-101, 1961.

JENIK, F.: Electronic neuron models as an aid to neurophysiological research. *Ergebn. Biol.* 25, 207-245, 1962.

KUPFMULLER, K., and JENIK, F.: Uber die Nachrichtenverarbeitung in der Nervenzelle. *Kybernetik* 1/1, 1-6, 1961.

PUMPHREY, R. J.: *Hearing. Symposia of the Society for Experimental Biology, Biological Mechanisms in Animal Behavior.* Cambridge University Press, Cambridge 1950.

REICHARDT, W.: Uber das optische Auflosungsvermogen der Facetten-Augen von Limulus. *Kybernetik* 1/2, 57-69, 1961.

REICHARDT, W., and MACGINITIE, G.: Zur Theorie der lateralen Inhibition. *Kybernetik* 1/4, 155-165, 1962.

RODIECK, R. W., KIANG, N. Y.-S., and GERSTEIN, G. L.: Some quantitative methods for the study of spontaneous activity of single neurons. *Biophys. J.*, 2, 351-368, 1962.

ROEDER, K. D.: Spontaneous activity and behaviour. *Scientific Monthly,* 362-370, 1955.

RUCK, P.: Electrophysiology of the insect dorsal ocellus, pt II. *J. gen. Physiol.*, 44, 629-639, 1961.

TASAKI, I.: Afferent impulses in auditory nerve fibers and the mechanism of impulse initiation in the cochlea. G. L. Rasmussen & W. F. Windler (eds) *Neural Mechanisms of the Auditory and Vestibular Systems. Ch.* Thomas, Springfield, *Ill., 1960.*

TAYLOR, *W. K.: Computers and the Nervous System. Symposia of the Society for Experimental Biology,* Number XIV: *Models and Analogues in Biology*, 152-168. Cambridge University Press, Cambridge 1960.

TAYLOR, *W. K.: Electrical Simulation of Some Nervous System Functional Activities. Information theory,* Third London Symposium, *314-328. Butterworth*, London 1956.

VARJU, D.: Vergleich zweier Modelle fur laterale Inhibition. *Kybernetik,* 1/5, 200-208, 1962.

VERVEEN, A. A.: *Fluctuation in Excitability.* Thesis, Amsterdam 1961.

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