NEURAL ANALOGS

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Introduction

Information processing in the nervous system is receiving increasing attention from researchers in the communications sciences. Stimulating and effective liaison between neurophysiologists and engineers is apparent on several fronts and is expanding rapidly.

It is presently popular to call such interactions between biology and engineering 'Bionics,' although it is not clear that much information is added by the term. Bionics is a formless sack into which a wide variety of strange bedfellows are thrown. Like Cybernetics, it represents the drawing together of many disparate fields, but actually constitutes no discipline in itself.

Basically there are two quite distinct areas of activity. In one the background and orientation of the engineering sciences are used to promote understanding of physiological systems. Here the concepts of information processing, computer operations, pulse coding, and digital and analog logic can be usefully brought to bear. A stimulating and catalyzing effect of the one discipline on the other has already occurred and is rapidly increasing. Sophisticated comprehension of nervous-system operation must ultimately depend on assistance from the communications sciences.

The other area of activity contains attempts to extract useful or at least suggestive information from biology (notably neurophysiology) to develop new approaches to communications and automata. The idea is that nature can provide cues, either from single elements or from entire systems, which can be useful to communication engineering.

Neural Analogs

One of the most prolific of these activities (certainly among the most vigorous) straddles both of the areas mentioned above. This is neural modeling. The art is not new; a simple electrical model was described over half a century ago.1* Simulation with chemical models2-7 followed, and more recently, flexible electrical analogs8-12 have appeared. Mathematical modeling, while necessarily constrained to oversimplification, has been extensive.9-17 Some of the mathematical models have been formulated by neurophysiologists to clarify and consolidate their findings.18-21 The advent of the high-speed digital computer has made it possible to explore small network behavior,22-25 although once again it has been found necessary to simplify greatly.

Two quite different kinds of neural modeling have resulted. It is the purpose of this paper to emphasize the differences between these two approaches, to review briefly some of the main streams of activity in neural modeling, and to show, by way of example, the results of one particular line of investigation - the work dealing with real-time electronic neural analogs.

In one category of neural modeling the intent is to investigate functions of the nervous system by simulating the parameters of the biological original closely. The analogs which follow from this philosophy may supplement physiological research in a unique way. They can provide a means of examining the possible operations of nervous structures which may not be easily explored in vivo. They can be used to test theories of neural organization, to discover functions of nerve cells not previously seen, and to investigate the information-processing properties of nervous tissue. They are valid only insofar as they contain enough modeling parameters of sufficient accuracy, and insofar as their actual and predicted behavior is in agreement with that of the living system. Very often such consonance is difficult to establish because of our incomplete knowledge of the nervous system. This is especially true of the brain itself. Perhaps our best hope at the moment is to try to understand what seems to be the simpler peripheral structures.

In the second kind of neural "modeling" the intent generally is to explore single-element logical behavior or the mass actions and self-organizing properties of ensembles of relatively simple, quasi-neural elements. The resemblance to biological neurons is superficial, the abstraction deliberately having been made gross and incomplete. Such systems may have intrinsic interest and application but should not necessarily be expected to yield physiological understanding.

Within this group, two subdivisions can be conveniently made. There are, for example, the mathematical models and computer simulations to investigate adaptive and self-organizing systems,26-32 and the analyses and the hardware analogs to explore logics of quasi-neural elements.33-37
The principal impetus for this line of investigation derives from the reputed great flexibility and computing power of nervous systems. It has been tempting to abstract some of the properties of neurons and to investigate the network behavior of elements having similar properties. It is certainly true that networks of nonlinear elements having modifiable interconnections can produce interesting behavior. Such properties as threshold firing, temporal summation, inhibition, and refractoriness lead to complex and intriguing results. It is also probably true that in the future such systems can be made to adapt to "experience" in ways that are useful and non-trivial. However, relevance to biological computers (brains and nervous systems) is by no means established, certain oracular pronouncements notwithstanding.

Several lines of investigation should be mentioned which are related to neural modeling but which cannot be categorized as such. Observations of the complex functions of nervous systems have led to the speculation that hardware analogs may be useful to computer technology. Consequently there has been some effort directed toward the development of new devices which incorporate some of the black-box functions of neurons.34,36,38

It is frequently presumed that analogs of neural mechanisms provide useful novelty in the engineering sense. This has by no means been established. In the first place nature has not yet shown us new engineering tricks; threshold devices, pulse logic, inhibition, and analog memory have been around for a long time. While it is true that some device development and some systems research have been spurred by contemplation of biological facts, no really new engineering secrets have been wrested from nature; the advances have resulted from the designers' ingenuity.

Another related area has to do with the testing and modeling of information processing in biological organisms; here the frame of reference is more nearly psychophysical than physiological. Some aspect of the behavior of an organism is analyzed, and a conceptual system is constructed on the basis of this analysis. The elements of the system are formal logical operators, not neural analogs. The model is then used as a basis for prediction and understanding of additional behavior. Novel and useful applications to hardware systems sometimes follow.39,40

Some Considerations of Neural Functions

There is often a strong temptation for non-physiologists to take an oversimplified view of the nervous system. Frequently such views arise from limitations imposed by our analytical tools, and the restrictions are candidly admitted. More frequently, however, oversimplified abstractions of nervous structures arise from an incomplete understanding of the immensity of the problem.

Let us briefly examine some of the information that neurophysiology and neuroanatomy have provided. Consider, for example, the human visual system. Reasonable estimates place the number of photoreceptors in each eye at 1.3×10^8, the number of interconnected elements in the retina at about 10^9, and the number of transmission lines to the brain (optic nerve) at 10^6. The entire brain contains something like 10^11 elements. If these estimates are in serious error, they very likely are too small. For example, recent electron-microscopic examination of the frog's optic nerve raised the previously accepted estimate of fiber count from 3×10^4 to 5×10^5 as a lower limit.41 Thus it is seen that the nervous system has many orders of magnitude more elements than our largest computers. But what about the complexity of each of these elements, the neurons?

Until about thirty years ago the neuron was thought to be a simple element. Its apparent "all-or-none" behavior led to the picture of an uncomplicated relay which fired off an electrical pulse when its input threshold was exceeded. This simplicity vanished with more knowledge. Discrete neural signals are now thought to be confined to the output (axon) portion of the cell. Furthermore, there is evidence that in many situations all-or-none responses are less significant than continuous (amplitude-variable) phenomena. Consequently, all-or-none phenomena have been relegated to a special case and, in the view of some neuropsychologists, even to a minor role.42,43

Both pulse and continuous activity are probably involved in the transmission of events from one neuron to another. When a cell fires, an action potential (all-or-none pulse or "spike") propagates along the axon. This pulse may be an isolated event, or it may be one of a train where the intervals are time-variable. To a first-order approximation these pulses are alike (100 mv, 0.5 msec). Propagation is an active process; each pulse is continuously regenerated as it traverses the axon.

Axons terminate at synapses, which are structurally discrete junctions between cells. With a few exceptions there appears to be no trans-synaptic pulse conduction. It seems that in most synapses a presynaptic pulse triggers a unique chemical response at the junction. Thus, an all-or-none pulse traveling along an axon dies as it reaches a synapse. Subsequently a postsynaptic potential is generated in the recipient neuron. This may occur either at a dendrite (input fiber) or at the cell body itself, depending on the site of the synaptic connection.

This new electrical event has a continuous range of intensity. It is a "graded" potential which flows slowly and with attenuation (unlike a spike), and it may last for many tens of milliseconds. Such a signal may either excite or inhibit the cell. Also, a given presynaptic fiber may either excite or inhibit at different
times, depending on the state of the receiving neuron. Firing of a neuron may depend on thousands of convergent inputs.

These and other complexities handicap comprehensive mathematical analysis of networks of neurons. For instance, there exists no analytical method for deducing the function of an anatomical structure from its geometrical or topological configuration. Also, there is some, but not much, direct evidence for synaptic change as a function of use; such evidence as does exist is incomplete and controversial. The entire subject of synaptic mechanisms is difficult and complex. Furthermore, practically nothing is known about the mechanisms of memory and learning. With regard to network connectivity, there is little evidence for randomness. Some striking evidence indicates that the visual system, for example, is anatomically highly specified, even at birth. Finally, it is important to realize that owing to difficulties of measurement, many of the input-output relations of neurons have not been directly observed - they are inferred.

This highly condensed account of neural action has been presented to show that neural events are far from simple, and that our knowledge is by no means complete. Several recent reviews give excellent and convincing accounts of the situation.

Now, what about our analogs? We must note that modeling implies abstraction which in turn often implies simplification. The descriptions of neural events given above include many subtleties, yet they omit many physiological facts. For example, despite the term "all-or-none", spike amplitude often is a variable; spike waveform and overshoot have many forms; baseline ("resting") potentials are functionally related to recent firing activity. Even the most accurate neural models ignore these and many other properties. It is generally assumed that such omissions are reasonably "safe" and that the ignored parameters lead to unimportant effects. If functionally accurate modeling is intended, such assumptions can be tolerated only so long as the behavior of the analog and the original are not divergent. In the case of quasi-neural modeling (as in the adaptive systems approach) where functional accuracy is apparently of little concern, the simplifications are extreme. Rarely, for example, are refractory recovery or the complicated synaptic transmission functions included.

Electronic Models of Neurons

Electronic neural analogs can provide a flexible means for exploring the operation of the nervous system. It is relatively easy to incorporate a large number of parameters representative of the biological cell. The model may then be used as an analog computer to examine functions that may be exceedingly difficult if not impossible to predict or to analyze fully. The studies described below take for their premise that such simulation can have validity and that continued exploration with such models can lead to a better comprehension of neural events. In most of these analogs a strong attempt was made to produce a reasonably accurate physiological representation.

One of the earliest electrical models was described by Walter in 1953. An array of gas-discharge lamps was made to behave in an axon-like manner. The system was devised to demonstrate all-or-none impulse propagation, facilitation, accommodation, and inhibition.

Burns introduced a thyratron model in 1955 to elucidate his electrophysiological investigations of repetitive firing in nervous tissue. He demonstrated the properties of after-discharges (sustained firing following stimulus removal) owing to interacting recovery mechanisms following conditioning stimuli. Once again the system was principally an analog of axonal mechanisms.

Meanwhile the quiet neurophysiological revolution described by Bullock was taking place. The relative importance assigned to axonal transmission and simple discrete neural action was dwindling. About this same time an evolution was also taking place. Neural modeling began to come into vogue.

In 1959, Harmon described a transistorized model of a neuron. In a subsequent analysis of the circuit (Harmon and Wolfe), it was shown how the parameters of threshold, all-or-none output, refractory recovery, inhibition, and repetitive firing could be made to approximate those of the biological neuron.

The following year an improved solid state neural model was reported by van Bergeijk and Harman. Two experiments were described in which the "neuromimes" (as they are now called) had been used to examine modes of information processing in the peripheral nervous system. In one, the "bug-detector" of Lettvin's frog's eye was modeled; in the other, dynamic range extension in the auditory system was explored.

In the same year Babcock examined in considerable detail the single-unit and small-network properties of a transistorized neural analog. Accounting for a large number of the physiological parameters, it was made to demonstrate a variety of interesting behavior. Included were summation, division, facilitation, counting, and frequency discrimination. In addition, a time-variable synaptic function was employed to obtain some primitive adaptive pattern recognition. This work underlies a current and quite interesting series of explorations of neural property-filtering (Babcock, et al.).

Küpfmüller and Jenik described a transistorized analog in which the input-output pulse relationships were analyzed in some detail. An interesting contribution of this model was...
its demonstration of the use of multiple inputs to obtain addition and multiplication.

An Example of One Approach

If one desires to simulate the biological neuron closely in the hope of producing psychologically meaningful results, the black-box equivalent parameters must be carefully chosen. Having produced a model, it is then incumbent upon the investigator to establish the validity of the analog; only then is it reasonable to expect physiological significance.

In the neuromime mentioned earlier,\(^5^5\) the operating parameters were made as consistent as possible with the corresponding biological values. Multiple excitatory inputs provide variable input integration characteristics to simulate gross aspects of dendritic behavior. Threshold is a time-varying function depending on the recent firing history of the unit. During firing, the model is absolutely refractory; after the output pulse, a decaying exponential return to resting threshold occurs. Inhibition can be introduced to negate excitatory influences. The model has a latency or transmission delay which varies with excitation level and firing frequency. Provision for accommodation and adaptation is readily made by simple external feedback loops. The basic circuit is relatively simple, containing five transistors, two diodes, two capacitors, and nineteen resistors.

The accuracy of the model was tested (Harmon\(^2^9\)) by replicating a number of classical neurophysiological experiments. As a result of these tests, properties such as time-intensity trade, burst firing, repetitive firing, accommodation, and transient change of excitability were shown to be consistent with those of the biological neuron. In addition, several properties were described which were built in by implication and discovered later, but for which no physiologically equivalent results have yet been found. For example, there is a pulse-deletion phenomenon which is due to asynchronous firing of one unit by another; this produces unexpected non-integral ratios of input to output firing frequencies. Future testing of such predicted behavior constitutes an interesting and challenging aspect of neural modeling.

A study has been made describing in detail the use of this analog to examine the dynamic range extension of the spiral innervation of the ear (van Bergeijk\(^5^9\)). In this work an attempt was made to deduce the function of a known anatomical structure; the problem concerns the ability of the auditory system to handle a dynamic range of 110 db, while a single neuron’s responses span only 20-25 db. A number of physiological experiments were suggested; results agree with predictions quite well.

The model has been used to explore a possible neurological origin of the flicker-fusion phenomenon (Levinson and Hummon\(^6^0\)). It was shown that a relatively simple configuration (apparently doing little violence to known anatomy and physiology) can with fair accuracy account for both physiological and psychophysical data. A prediction of a new psychophysical effect made on the basis of the model was reasonably well confirmed; this effect deals with human response to a flickering light of complex waveform.

Although our neuromimes are only models, and as such will never be more than rough approximations to the living cell, the accuracy of approximation is good enough to enable us to study several problems in neurophysiology. These investigations have been successful, not in leading to an end point, but rather in suggesting a number of new experiments, both in physiology and in psychophysics.

Conclusion

Modeling of the nervous system is expanding and is diversifying. Present efforts can be roughly divided into two schools. In one, the intent is to produce models which represent biological function as closely as possible and which we hope can be used to extend neurophysiological investigations. In the other, the idea is to explore the behavior of quasi-neural elements, to describe and analyze the behavior of devices having some of the gross functions of neurons.

Electronic analogs designed for accurate representation provide a flexible means for investigating properties of the "biological computer". It is not claimed that such models are complete or even exceedingly precise. The present state of neurophysiological knowledge itself precludes this. Rather, sufficient approximations exist to yield interesting and possibly useful functional equivalence. It would appear that neural modeling, if done realistically and checked closely by physiology and psychology, has considerable power in aiding our comprehension of nervous structure and function.

It can be shown that a considerable number of properties inherent in the living cell are present in some of these models without having been explicitly built in. One might speculate that a valid theory of neural operations could be based on a relatively simple set of explicit parameters. If so, the hope is raised that fundamental understanding of nervous system operation may be less complicated than the present mass of experimental data seems to suggest.
References


