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Biological Neural Networks As Model Systems For Designing Future Parallel Processing Computers

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One of the more interesting debates of the present day centers on whether human intelligence can be simulated by computer. Some [1-3] argue that there is something unique, or even mystical, about the human mind, so that intelligent behavior cannot be simulated by machine [1, 2]. Others [4] disagree on the premise that brains, on which minds depend, are simply collections of neurons and, since neurons are physical entities, they can be understood in physical and even mathematical terms, perhaps not soon, but in the foreseeable future. In an interesting discussion of this debate, Denning [5] points out that regardless of the questions raised by philosophers, investigators will continue to explore the possibility of producing thinking machines by building increasingly sophisticated systems.

In my laboratory, we work under the premise that neurons individually are not smart at all. Rather, they are physical units which are impinged upon continuously by other matter that influences the direction of voltage shifts across the units' membranes. Some influences are in the direction of depolarization (excitation) and others are in the direction of hyperpolarization (inhibition). In one type of neuron, the machinery of the cell responds in analog fashion to these incoming signals as spatio-temporal events that may or may not result in overcoming a threshold. If threshold is overcome, the cell responds digitally by initiating patterned, electrical impulses that are conducted along the axon to its terminals, usually some distance away. There, the impulses result in probabilistic, quantal release of neurotransmitter [6] at one or more synaptic sites on other neurons. The specific actions of the various spatio-temporal inputs on the postsynaptic cells again determine their responses. In a different type of neuron, the cell does not discharge impulses but spreads the response electrotonically along its membrane to synaptic sites. Neurons of this type function locally in the network and appear to be extremely important in information processing.

It is only in the actions of a great many neurons, billions in the case of the human nervous system, that intelligent behavior emerges. The enormous number of constituent parts and the complexity of the connectivities are the bases for doubts that the nervous system can be understood and simulated by computer. A common argument is that we would gain more insights by approximating biological neural networks as we think they might exist rather than by attempting to learn from them by rigorous study.

The problem with this approach is that, in the end, it will not bring us to our ultimate goal. Extrapolating from generalization to generalization removes us that much farther from understanding the bases for biological system robustness, memory, learning and intelligent behavior. Such extrapolations may produce more powerful machines than exist today, as Denning [5] has suggested, but they will fall far short of the desired end point of a truly thinking machine.

What is required to understand even the simplest neural system is a painstaking analysis, bit by bit, of the architecture and the physiological functioning of its various parts. The goals should be to gain insight to those features that are fundamental to all neural networks and then to develop the algorithms that define the responses. This kind of effort will result in new applications of biological system attributes to artificial systems and will result in advances in computer design. The research does, however, require the interaction of neurobiologists, neurophysiologists, physicists, modelers, mathematicians and theoreticians; in short, a formidable array of specialists. It also requires the development of highly specialized computer technologies. At the NASA-Ames Biocomputation Center, we have a team assembled to promote the technology required to understand the neurobiology, both in its own right and as a guide to future computer advances. We are also working to achieve the physical and mathematical interpretations essential to develop a silicon chip for potential inclusion in robots.

The biological neural networks we study, the vestibular utricular and saccular maculas of the inner ear, are among the most simple of the mammalian neural networks to understand and model. At the same time, they are complex enough to be useful for deriving principles of neural network organization. Because the basic organization of vestibular maculas does not differ between species, we have used the rat utricular macula as the model mammalian system.

Macular endorgans function as linear bioaccelerometers. Not surprising to engineers, maculas consist of a test mass above a detecting unit. The test mass, suspended in a weak gel-like liquid, consists of tiny crystallite particles (otoconia) that are unevenly distributed above the detector. The underlying detecting unit is a neural network structurally organized for weighted, parallel distributed processing of information. The network consists of two kinds of hair cells (type I and type II), a system of nerve endings with branches and collaterals, and a number of small-diameter nerve fibers that end on type II hair cells and on other neural elements within the macula. The network is not identical in detailed organization from site to site, and there may be a match between otoconial loading and network properties [7]. If so, parallel processing of acceleratory information begins at the input, otoconial layer even though it is a non-neural entity.

The hair cells function as detectors. They bear a tuft of thread-like processes, called stereocilia, and a single kinocilium at their apical surfaces. The stereociliary tufts are always organized in hexagonal arrays, but the size and height of the individual stereocilia, as well as their number, differ from site to site. Ordinarily, the stereocilia are in staircased order, with the tallest bordering the kinocilium, which is the tallest of all. The kinocilium is attached to the otoconial layer by strands of organic substance. Since the kinocilium has been shown to be capable of motility [8], we believe it agitates the otoconial layer. Translational linear acceleratory force affects the otoconia differently, according to their individual masses and the background of activity already going on. The result is that complex waves are constantly being emitted, with or without the addition of transient accelerations, and the detecting units respond according to their stereociliary configurations.

Fourier analysis of various tuft organizations shows that the stereociliary tufts are highly directionally tuned by their hexagonal organization and their specific stereociliary heights [9]. In another astonishing correlation to human-engineered devices, it seems that nature invented the equivalent of a sensitive phased array antenna millions of years ago! Analysis of the repeating lattice angles of stereociliary tufts demonstrate that they range between 115^{o} and 125^{o} [10, 11]. The optimum repeating lattice angle for human-engineered antennas is a 120^{o} rhombus [12].

These and other findings mean that we are well on our way toward understanding, and expressing in mathematical and engineering terms, the basis of detection of incoming linear acceleratory signals by this biological system. Achieving an understanding of the neural network organization is also well underway, using computer technology and specially developed software [13] to reconstruct actual parts of the network and to produce symbolic models to mimic their functioning. This research currently is tedious and labor-intensive, requiring photography of serial sections in a transmission electron microscope, reassembly of the micrographs into montages of the sections, tracing objects of interest from the montages, digitizing the tracings into a computer, and reassembling the tracings into shaded solid and transparent images. The research would be greatly expedited by semiautomation of data collection to eliminate photography completely. At NASA's Biocomputation Center, we are working to advance this technology. Achieving the goal of semiautomatic data collection and reassembly will be a breakthrough for neuroscientists trying to understand the architectures of more advanced biological neural networks and for scientists wishing to apply insights obtained from biological systems to advance parallel processing computers and robotic devices.

Using current reconstruction techniques, we have been able to demonstrate the smallest functional units of the network, its receptive fields, which consists of the calyceal ending(s) of a nerve fiber together with all the hair cells that synapse with it (them). We have also reconstructed small parts of the neural network. The basic findings are that no two of the receptive fields are identical and that the network varies in complexity from site to site [14, 15].

Type I cells are enclosed by the calyces and synapse only with them. Type II cells lie outside the calyces and distribute their output to as many as four neighboring calyces by synapsing either with the calyces or with calyceal collateral processes. Calyceal collaterals are either presynaptic (feedforward), postsynaptic (feedback), or reciprocally (bidirectional) synaptic to type II cells. Feedforward collaterals end opposite subsynaptic cisterns, strongly suggesting that the collaterals have an inhibitory action (they hyperpolarize the type II hair cell) (discussed in [16]). Experimental evidence [17, 18] indicates that synaptic junctions with subsynaptic cisterns function in long-lasting hyperpolarization of the postsynaptic cell. The findings strongly suggest that type II hair cell activity is dampened when calyces and their processes are activated

(depolarized), possibly providing for a center-on surround-off response that is well known in the retinal neural network.

In addition to the vestibular nerve fibers just described, there is a system of small, beaded fibers (efferents) that arises extrinsic to the macula and is presynaptic to all the other neural elements except for type I hair cells. The nerve fibers wander through the macular neuroepithelium where their beads, more accurately their "boutons", synapse with type II hair cells, calyces, collaterals, nerve branches and branch junctions. Morphological and experimental evidence strongly suggests that the endings on type II hair cells, which have subsynaptic cisterns, provide a background of inhibition (hyperpolarization) of the type II hair cell, while the remaining endings on other neural elements provide background excitation (see [16] and [17]). One bouton may synapse with both a type II hair cell and a calyx, so that the specific function of the synapse appears to be determined by conditions on the postsynaptic side.

In a broader context, because all the synapses likely release transmitter substances quantally and perhaps with nonuniform release probabilities [6], the dynamics of the functioning network are likely nonlinear. The salient question is whether we can reduce the complexities of the neural network just briefly described to meaningful engineering and mathematical expressions that capture, uncompromisingly, the architectural and functional foundations of the system without simply reproducing it. For if we are to improve artificial computer technologies and produce thinking machines, we must be able to accomplish this without replicating the billions of neurons and their connectivities present in a human brain. We must reduce brain organization to its basic organization and build from there. Perhaps in some ways the artificial brains can be made to outstrip the biological!

As part of this effort, we have produced a dynamic, symbolic model [18] of the functioning of a small part of the neural network (Figure 1). This model is based on mathematical interpretations of the neural geometry revealed by the reconstruction work. In the initial, six-tiered model shown here, three different geometric arrangements were incorporated in a two-dimensional model. The layers depicted in order are 1) stimulus, 2) type I hair cells, 3) type II hair cells, 4) calyces, 5) impulse initiation zone, 6) neuronal discharge. The output, patterned neural discharge is also displayed on the screen. On the computer, dynamic states are depicted in a range of colors, from blue (maximal inhibition) through green (neutral) to red (maximal excitation). Comparable states in Figure 1 are shown as shaded symbols (see legend). The effects of varying individual parameters, such as direction of input, hair cell polarization, length of nerve branches, and resting discharge rate, can be determined quantitatively and qualitatively by the model. Feedforward and feedback loops are now being added to study the effect of lateral inhibition on the output of the various receptive fields. Still another addition is conversion to a three-dimensional model and putting in place the background activity imposed by the small-diameter efferents.

While much remains to be learned from more advanced versions of the model, we already have found that inhibition is important in a neural network. When all elements are excitatory, the simulated network quickly saturates so that all units stay on continuously. Only when inhibition is introduced, in our model at the level of the type II hair cell, does neural coding appear. It is also apparent from the model that branching over short distances makes the unit more sensitive to different inputs at its calyceal sites (unit b in Figure 1), leading to a more irregular discharge pattern. Lengthening the branches tends to make the unit more regular in its responses.

In complementary models, we have been able to reproduce the receptive fields of vestibular maculas by the Monte Carlo simulation method [16]. That is, we derived constraints such as the number of type I and type II hair cells and the number and lengths of the nerve fiber branches in the various kinds of fields. Probability tables derived from these constraints were used together with a random number generator to reproduce examples of biological receptive fields by computer. The results of this method strongly suggest to us that biological neural networks develop by constrained randomness in wiring and are not entirely genetically determined. In future research, we hope to design artificial neural networks entirely by constrained randomness to learn whether a degree of randomness in wiring might be beneficial to artificial systems.

As we continue to develop our simulations, we also are beginning to reduce the macular architecture to symbolic block diagrams. Figure 2 illustrates one of these diagrams, for a highly branched nerve fiber. Next, these block diagrams will be reduced to electronic circuit diagrams, using small and medium scale

integraterd circuit devices (SSI and MSI), for implementation in hardware. Development of a prototype linear accelerometer chip based on its biological counterpart should be possible in the next few years.

In the meantime, what are the particular attributes of biological neural networks that could help us to design better parallel processing computers? One major observation is that the nervous system appears to be organized on the basis of two circuits: highly channeled and distributed modifying [16] (Figure 3). That is, there are highly directed [19] inputs to an area, carrying highly specific information, but the information is processed further by local or intrinsic circuits that modify the output to another station. The first to suggest such a basic organization was Shepard [20], who used the less definitive terms "vertical" and "horizontal" for the circuits. Because we now find that part of the distributed circuit functions to dampen type II hair cell activity following calyceal voltage changes, it is possible that lateral inhibition is also a fundamental feature of distributed modifying circuits (see also [18]).

Our research suggests, however, that a third kind of circuit may exist. This is a system of nerve fibers that comes into an area or layer from another site and provides a widely distributed, biased background of activity against which the channeled and distributed modifying circuits operate. In natural systems, it is possible to raise or lower background activity hormonally, by increased input to it or through local, reciprocal control as occurs to some extent in the gravity receptor. That is, heightened activity in a neuron could release neurotransmitter to terminals of reciprocal type, activating them to modulate the responses of more distant neurons. This kind of circuit might prove essential to learning, cognition and creativity, as it could help focus attention to certain incoming information, correlate neural activity over variable distances, and result in disregard of other simultaneous inputs that might otherwise be distracting. In the human brain, such circuits may provide the emotional context within which higher cognitive functioning takes place (see also discussion in [3]). While for now the conservative approach is to consider this group of fibers as part of the distributed modifying circuitry, the background activity these fibers provide may prove sufficiently significant to demand recognition as a separate, third kind of fundamental circuitry.

Other factors that appear to be important for incorporation into artificial neural networks and computer technologies are the following: 1) Biological neural networks are not modular. Variation in receptive field and network organization is apparently important to parallel processing of incoming information, to segregate discrete parts of the message for different distributions. 2) Biological systems are robust and tolerant of neuron failure. Robustness is achieved in part through redundancy, but likely also through non-modularity and constrained randomness in wiring. 3) Individual neurons are tiny bits in the machine of intelligence. They are not smart enough to be able to tell another neuron that it is responding in error. Thus, backpropagation as described and utilized in engineered neural networks does not exist in biological systems. However, feedforward-feedback loops and lateral inhibition may be essential to neural functioning. 4) Constrained randomness in wiring may be typical of all advanced biological neural networks. This and other probabilistic features of biological neural information processing systems suggest that natural neural networks are dynamically nonlinear.

While we still have a long way to go to understand even this most simple mammalian neural network in sufficient detail for extrapolation to computers and robots, a start has been made. Moreover, the insights we are obtaining and the technologies we are developing should help advance our understanding of the more complex neural networks that underlie human intelligence. Progress in this area should, as Denning [5] suggests, lead to ever more sophisticated machines.

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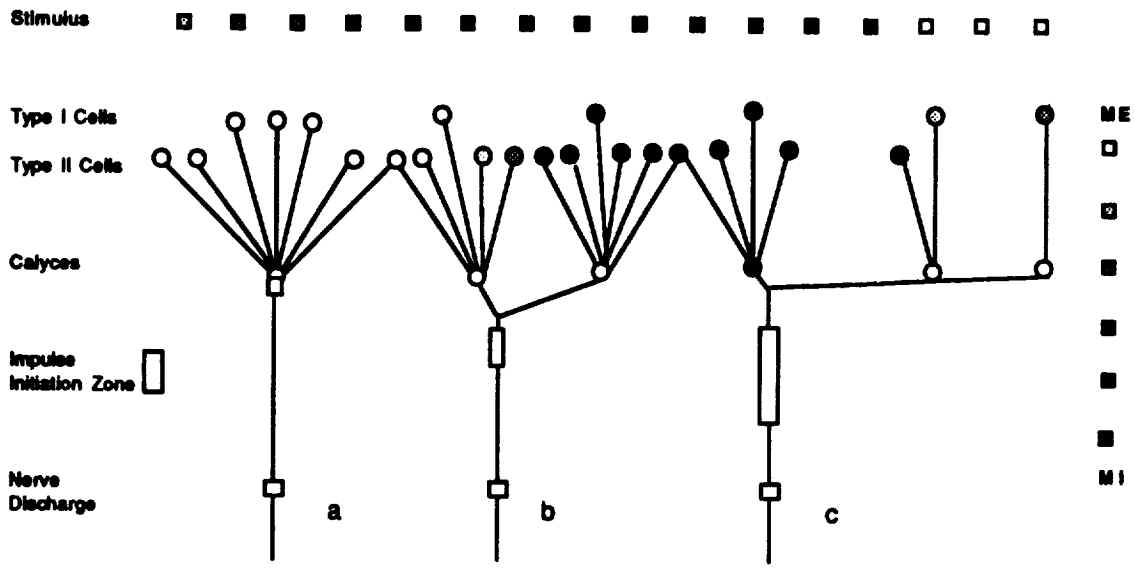

Figure 1.

This figure illustrates our dynamic, symbolic model of a functioning macular neural network. See text and legends at right and left for explanation of the model. MI, Maximum inhibition; ME, Maximum excitation.

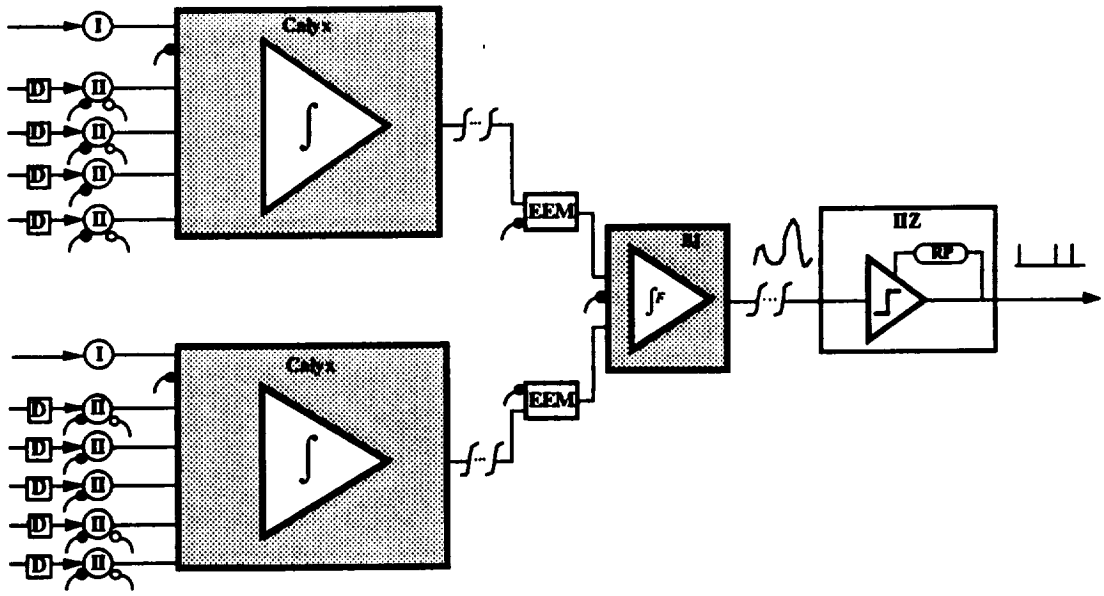

Figure 2.

Figure 2 is a symbolic block diagram of a macular nerve fiber with two branches. The symbols are: I, type I hair cell; II, type II hair cell; filled circles at the ends of curved lines, efferent terminals of extrinsic origin; open circles at the ends of curved lines, intrinsic efferent endings; BJ, branch junction; D, delay; EEM, extrinsic efferent modification of voltage spreading along the nerve fiber; IIZ, impulse initiation zone; RP, refractory period; /.../ more of the same. The black lines represent the nerve fiber and its branches (like wires, except for the slow propagation time). The integrator symbol inside calyceal triangles indicates simple integration of the inputs; an integrator symbol plus *F* (in BJ) indicates integration of a function of the inputs. The symbol inside the triangle at IIZ represents a threshold comparator. The undulating line above the nerve fiber between BJ and IIZ indicates that variable continuous voltage, an analog signal, is carried by the nerve fiber up to this point. The analog signals are converted to pulse trains at the IIZ. These are digital signals (pulse trains at far right).

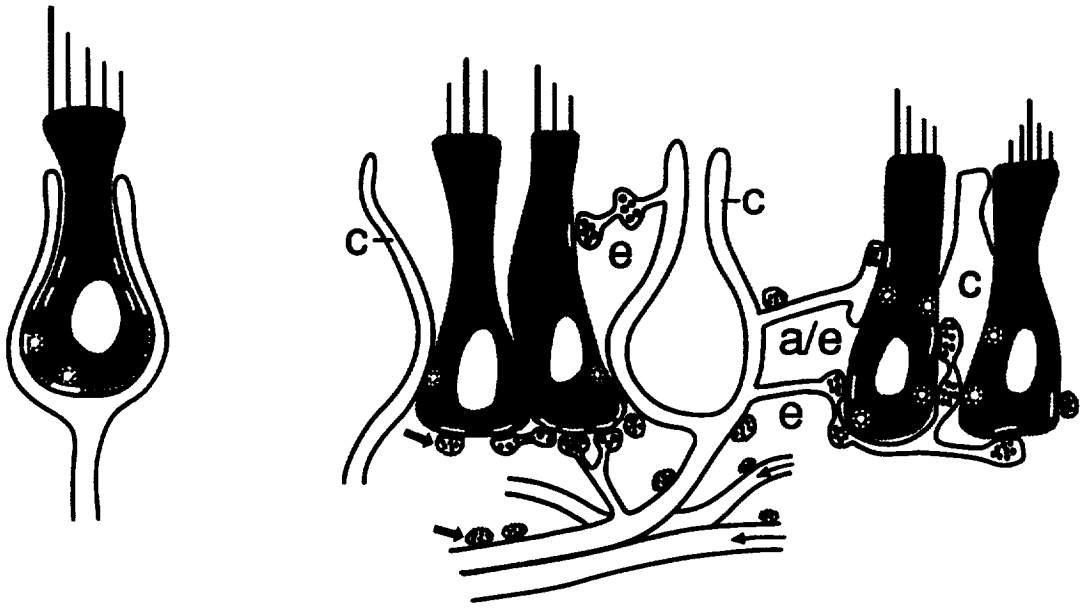

Figure 3.

This diagram illustrates the concept that certain inputs to a neural network are highly channeled, or directed, to a second unit while other parts of the network are concerned with distributing modulatory effects to nearby and more distant units. In this way, the output of the system is modified. I, type I hair cell; II, type II hair cell; a/e, afferent/efferent, or reciprocal endings; c, calyx; e, efferent-type collaterals; asterisk-like symbols, ribbon and spherular synaptic junctions; clear bars in type II and type I hair cells, subsynaptic and subsurface cisterns, respectively. Fine arrows show direction of information flow; heavy arrows indicate efferent terminals of extrinsic origin.