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Implications of Dendritic Models for Neural Network Properties, a small, intensive workshop focussing on the experience and insights gained by participants in their mathematical and computational studies of neuron models which are realistic in the sense that they preserve some of the distributed anatomy and some of the nonuniform, nonlinear membrane properties of biological neurons.

Most of the participants were experienced both in physics and in experimental neurophysiology; all shared a conviction that dendritic synaptic input patterns and membrane nonlinearity are important in actual biological neural networks. In addition to discussion of recent experiments and computations, attention was given to identifying collaborations that could offer special promise of demonstrating how network properties can be enriched by including realistic neuron properties in network models.

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**Report to the Office of Naval Research on
The Santa Fe Institute Workshop
Implications of Dendritic Models for Neural Network Properties
October 10-14, 1991**

"Implications of Dendritic Models for Neural Network Properties", a small, intensive workshop was held at the Santa Fe Institute in October, 1991. Organized by Wilfrid Rall (Mathematical Research Branch, NIDDK, National Institutes of Health), this workshop focussed on the experience and insights gained by participants in their mathematical and computational studies of neuron models which are realistic in the sense that they preserve some of the distributed anatomy and some of the nonuniform, nonlinear membrane properties of biological neurons.

Most of the participants were experienced both in physics and in experimental neurophysiology; all shared a conviction that dendritic synaptic input patterns and membrane nonlinearity are important in actual biological neural networks. In addition to discussion of recent experiments and computations, attention was given to identifying collaborations that could offer special promise of demonstrating how network properties can be enriched by including realistic neuron properties in network models.

John Miller (U.C. Berkeley) and his collaborators have excellent anatomical and physiological data on the receptors and the interneurons which process information about wind-direction (in crickets). They have shown how the overlapping receptive fields are used to obtain high resolution. Miller discussed how they have applied information theoretic methods (similar to the linear filter analysis of Bialek, and the principal component analysis used by Richmond and Opticon) to analyze the remarkable performance of this experimental system. He and others discussed implications for studies of other neural systems.

Larry Abbott (Brandeis) discussed a reduced dendritic neuron model in which synaptic excitation and inhibition were assumed to sum linearly at distal dendritic locations, but proximal dendritic locations were assumed to receive synaptic inhibition characterized by significant membrane shunting. He discussed how the nonlinearity contributed by this proximal inhibition is responsible for important network properties; in particular, it can prevent the pathology of oversimplified nerve nets whose activity evolves either to maximal activity or no activity. This reduced model was discussed in relation to the experimental knowledge and insights of many participants .

Idan Segev (Hebrew Univ. Jerusalem) presented several interesting results of modeling studies done with his collaborators in Jerusalem. These included some rather general mathematical results about the time delays to be expected between the centroid of an input transient at one dendritic

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John Rinzel (NIH) presented a dynamical systems analysis of the effects of both weak and strong coupling between a pair of cells having nonlinear membrane properties. One example showed that endogenous bursting cells, when coupled by weak gap junctions, can synchronize but with the burst period substantially increased. Another example showed how retention of near-threshold behavior of repetitive spike generation, allows one to capture a network mediated bursting oscillation between two non-endogenous bursters, one excitatory and one inhibitory. Such phenomena would be lost if one assumed an ad-hoc monotonic input-output relation for each cell.

Charles Wilson (Univ. Tennessee Center for Health Sciences) presented experimental data and modeling studies for neostriatal spiny projection neurons. He focused attention on inward rectification at membrane potentials near the potassium equilibrium potential, and how this can be understood in terms of a potassium channel that is very rapidly activated as the cell is hyperpolarized. Using a compartmental model, he fitted the parameters of this channel to the whole cell input resistance, time constant, and membrane potential values observed in tissue slices. He showed that when synaptic inputs were distributed widely over the dendrites, they would sum cooperatively until the overall level of depolarization exceeded a point at which the synaptic nonlinearity overcame the effect of inward rectification (this was usually near the firing threshold for the neuron). This contrasted significantly with the synaptic nonlinearity found when synaptic inputs are spatially clustered. He also discussed a shift in channel behavior (with potential) that underlies a shift between two different behavioral states of such neurons.

Julian J.B. Jack (Oxford Univ.) presented some of the results that he and his colleagues have achieved in modelling pyramidal cells of cortex and hippocampus. They have worked with complete anatomical reconstructions, and have demonstrated the complete separation of variables solution for detailed models of such neurons; this solution has also been programmed for efficient computations. They have used both whole cell patch clamp and sharp electrodes, and find that soma shunting is significant with the sharp electrodes. They have concluded that simple linear modeling is inadequate to fit experiment, and have started to develop reduced models which incorporate voltage-dependent conductances as well as synaptic conductances.

William R. Holmes (Ohio Univ.) presented the results of a set of computational experiments which contrasted different spatio-temporal patterns of synaptic input to the dendrites of a modelled dentate granule cell. These patterns involved permutations of 5 time steps and dendritic locations that were mid-dendritic and/or distal dendritic, either on different branches or on the same branch; these were done with and without the presence of voltage dependent channels on proximal dendrites and with and without the presence of NMDA receptor mediated conductances co-activated with the synaptic input; (120 cases in all). In each case, he asked if the input caused the neuron to fire an action potential, and if so, when? In general, the results met expectations with regard to distal/proximal timing, and enhancement by voltage dependent conductances, but the variation in the delay to spike time demonstrated subtle differences that could not be captured by the oversimplified models used in most neural networks.

Thomas M. McKenna (ONR) provided a comprehensive review of the research supported by the "Single Neuron Computation" program that he has developed for ONR; this included many individual research projects, some familiar to the group, others less familiar. He also discussed some results of their Biological Neural Network Program, as well as his list of scientific issues .

Wilfrid Rall (NIH) reviewed briefly two computational demonstrations of how spatio-temporal patterns of synaptic input might be distinguished. Using a chain of ten compartments to represent a dendritic tree, an early computation showed the difference between a distal-to-proximal input sequence and a proximal-to-distal sequence of equal synaptic inputs; this could provide a basis for movement detection, or other spatio-temporal sequence detection. A recent computation (with Segev) showed differential effects of spatio-temporal patterns of synaptic inputs to excitable dendritic spines on distal dendritic arbors of neuron models with many branches and many dendritic spines. He noted that not only such spatio-temporal patterns, but also nonlinear dynamical system properties of cable-coupled regions (with different channel densities), as well as dendro-dendritic synaptic coupling between dendritic arbors, all offer rich possibilities that are completely neglected when a neuron is represented as a single node in a network. He concluded by urging that we consider the challenge of identifying particularly good examples where computations could demonstrate how a particular network composed of dendritic neuron models could perform some interesting task, robustly, and then show that when the dendritic compartments and synapses are collapsed to a single node, the interesting task is not performed.

Bryan Travis (Los Alamos NL) presented fascinating glimpses of an unusually comprehensive computer program that he has developed to represent populations of neurons connected synaptically in accord with much neuroanatomical data. His program provides the possibility of simulating realistic neuronal systems on the Cray, and he seems already to have incorporated much

relevant data for an auditory system, a cerebellar system, and (with Valerie Gremillion) a visual system. Many of the workshop participants felt a strong interest in the possibility of collaborations to explore the computational consequences of variations in the specification of synaptic connections and strengths.

Valerie Gremillion (Los Alamos NL) discussed the mammalian visual system, and considered what kinds of questions to ask and simulations to try to carry out on the Cray by means of Travis' computer program. She communicated interesting perspectives and strong motivation to explore questions of the kind fostered by this workshop .

Andre Longtin (Los Alamos NL) presented his modeling approach to the encoding of information in the auditory system. He wishes to assess the role played by noise in the encoding process, especially the possibility of stochastic resonance effects. With Bryan Travis, he hopes to explore the implications of feedback to the outer hair cells in a realistic model of the auditory system.

Likely collaborations to result from this meeting are: Abbott & Rinzel: on nonlinear dynamics of neurons; Abbott & Miller: on information theoretic approach to neural coding; Julian Jack & Valerie Gremillion: on some aspects of modeling of synaptic inputs to pyramidal cells of visual cortex; Jack Wilson: on the non-uniqueness in fitting simple neural models to experimental data, especially when anatomical structure is excluded; Wilson, Travis & Gremillion: on exploring computations that incorporate Wilson's experimental data in Travis' comprehensive computer program; Miller, Bialek & Longtin: on exploration of stochastic resonance; Segev & Rinzel: on axon propagation involving varicosities; Segev & Rall: on reduced neuron models preserving essential nonlinear dendritic processing; Travis & Rall, (perhaps with Holmes & Segev): on testing effects of reduced models in the system Travis has programmed; Travis & Longtin: on exploring effects of noise introduced into auditory processing.

Another, more general, result of this meeting was acknowledgment of the need to actively develop the field of theoretical neurobiology. To that end an active working group in this area is being formed at the Santa Fe Institute. A modest amount of ONR funds were used to support staff time planning this outgrowth endeavor.