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Reply to Grossberg

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In response to comments by Grossberg, we discuss some topics related to neural models. We consider some experimental evidence from neurophysiology and neuroanatomy that bears on the simplifying assumptions that must be made when nervous system models are developed. A simple numerical example of a neural model with feedback is presented and discussed.

As we tried to point out in our recent article (Anderson, Silverstein, Ritz, & Jones, 1977), the approximations we made there were oversimplifications of the complex reality of the nervous system—made so we could discuss only a few aspects of a very difficult problem.

In Anderson et al. (1977), we considered a model that is partially linear. Whatever their theoretical shortcomings, linear systems approximate *some* aspects of neuron behavior surprisingly well. Clearly, many aspects of nervous system operation cannot be explained with linear models. We made the suggestion that a linear model, combined with a simple nonlinearity, gives rise to an interesting, relatively understandable nonlinear model with some intriguing applications to psychology. Grossberg (1978) obviously disagrees with some of our approximations. Below we make some comments that may clarify the biological basis of our model, and we also make a few remarks about the model itself.

Cell Properties

Many of the criticisms Grossberg (1978) makes of our approach seem to arise from use of his Equation 1, the active cable equation, as the basic descriptor of neuron behavior. This equation is of great importance to cellular neurophysiology. When appropriate forms for the conductances are inserted, it is the well-known Hodgkin–Huxley equation. Usually the potentials V_+, V_-, and V_p are taken to be potentials referring to points of thermodynamic equilibrium for various ionic species. In the references given by Grossberg, this is the case (see Equation 4, p. 87, of Hodgkin, 1964), and the equilibrium potentials V_+, V_-, and V_p correspond to sodium, potassium, and the so called "leak" conductance, which is "relatively unimportant" (Hodgkin, 1964, p. 87) and which gives currents carried by other ions.

We must emphasize that the parameter of activity we used in our model is related to cell *firing rate* and not directly to the potential. The equilibrium potentials are not closely related to the "saturation" that we were discussing in our article. The saturation (perhaps "limiting" might be a more descriptive term) referred to the cell's firing rate in response to its inputs. We made the approximation that a cell's response to its inputs was linear over a range of output firing frequencies. Outside the range, the output firing rate of the cell did not reflect changes in the amplitudes of its inputs. That is, limits were placed on the maximum and minimum firing rates of the cells, and there was a linear input–output relation in between. Since action potentials are the specializations used by nerve cells to transmit information over all but the shortest distances, firing rate is usually the most biologically meaningful parameter of cell output.

When a cell fires at maximum rate or does not fire at all, its membrane potential can be far from equilibrium potentials. In fact, if the V_+ in Grossberg's Equation 1 is taken to be V_{Na}, it often cannot even be approached by excitatory synaptic inputs. The excitatory acetylcholine synapse at the frog neuromuscular junction has a reversal potential around zero millivolts, since it increases conductance to both sodium and potassium ions,

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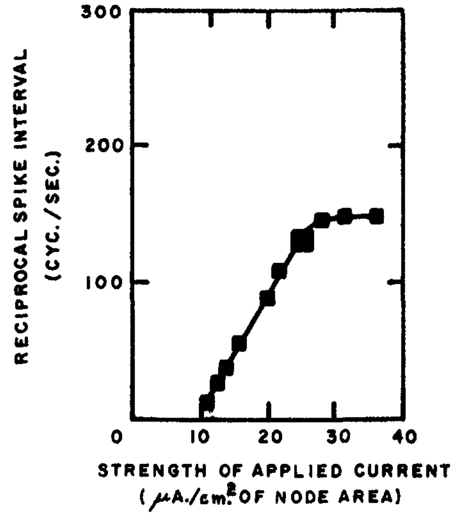

Figure 1. Curve of the reciprocal mean spike interval in response to a maintained depolarizing current of 1-sec duration and of increasing strength for a Class I crab axon. (This is a portion of Chapman's, 1966, Figure 3. Adapted with permission from "The Repetitive Responses of Isolated Axons From the Crab, *Carcinus Maenas*" by Reginald A. Chapman, *Journal of Experimental Biology*, 1966, *45*, 475–488. Copyright 1966 by the Company of Biologists.)

while the sodium equilibrium potential is considerably above zero.

The resting potential of a cell in the absence of inputs is often near the potassium equilibrium but rarely at it—otherwise, one would not see the negative potentials so characteristic of inhibitory postsynaptic potentials. Details of the ionic interactions vary from cell to cell, but the observation that points of zero and maximum firing rate rarely correspond to equilibrium potentials seems generally correct. Calvin (1972) comments that a change in membrane potential of 30 millivolts to 40 millivolts suffices to drive the firing frequency of a spinal motor neuron from one end of its dynamic range to the other.

The exact behavior of a neuron depends critically on the conductances and may vary widely depending on the values of the parameters. As one example, a set of simulations by Shapiro and Lenherr (1972) studied the responses of a computer model of the Hodgkin–Huxley equation. When they used parameters like those found in the squid axon, the system did not respond to a constant current stimulus until a threshold was reached. Then, the cell firing rate started at a high value and leveled off in a negatively accelerated curve as input current increased. When the parameters of the model were varied, particularly the time constant of the potassium system, the model neuron showed a much more linear relation between firing rate and magnitude of constant current stimulus.

Another example of interest is the repetitive response of the crab motor axon to maintained current stimuli. Figure 1, adapted from Chapman (1966), shows the reciprocal mean spike interval (close to, but not identical with, average frequency) for a current stimulus of 1-sec duration plotted against stimulus current. Figure 1 shows data from what Chapman called "Class I" axons, which responded with prolonged repetitive activities over a wide range of currents. "Class II" axons fired high-frequency bursts of action potentials, but the reciprocal mean spike interval during the burst showed a very similar pattern to Figure 1. ("Class III" axons seemed to be in poor physiological condition.)

The upper and lower limits on firing rate, seen clearly in Figure 1, coupled with a region of linear response, are of interest in light of our assumption of something very much like this in our model. We might also observe that the upper limit, where the cell no longer increased firing rate with increasing stimulating current, is far from any equilibrium point. The cell is capable of firing very much faster than its maximum response rate to maintained stimuli—about 150 spikes per second for Class I axons and about 240 spikes per second for Class II axons With trains of very brief current stimuli, it is possible to elicit maintained frequencies as high as 550 spikes per second.

Many sensory receptors show a surprisingly linear transduction of generator potential into firing rate. Several examples are discussed in a review article by Fuortes (1971). The generator potential is often not linearly related to the physical stimulus; often there is a logarithmic or power law relation between generator potential and physical magnitude. However, the voltage to frequency conversion of the spike generating region often is linear.

Membrane parameters and properties are suited to the system of which they form a part. The squid giant axon presumably shows its immediate jump to a high firing rate because it is a "command" fiber that initiates an escape reflex, which is an all-or-none response to dangerous situations (Brown, 1975). In sensory systems, it seems to be important to maintain a degree of linearity.

Grossberg is particularly concerned in his comments with the automatic gain control properties of neural networks. We should emphasize that we, in our article, were interested in the transient response of a set of very simple neuronlike elements. The gain control and the transient response may involve very different mechanisms. It strikes us as unlikely that it is desirable—or perhaps even possible—to account for both with the same model. In the visual system, adaptation involves changes at the levels of the photoreceptors, the operation of a complex set of neural interactions, and even the operation of a variable aperture (the pupil; Pöppel, Held, & Dowling, 1977).

The visual system is a particularly rich source of well-studied neural interactions. Possibly the best-known and most complete linear analysis of a part of a nervous system is the *Limulus* eye. This simple visual system can be modeled quite well as a linear system (see Knight, Toyoda, & Dodge, 1970). The vertebrate retina is more complex but contains important linear components as well as some nonlinearities. The extensive discussion in Graham and Ratliff (1974) provides a good review of linearity and nonlinearity in parts of the visual system. Some of the nonlinearities in vertebrates are "simple," such as the limiting we assumed in our model (Anderson et al., 1977). These nonlinearities are generally easy to deal with, but some appear to be more complicated. However, the X-cell system in cats, which seems from a number of lines of evidence to be concerned primarily with form vision, seems considerably more linear in its properties than the Y-cell or W-cell system.

The semicircular canal system can display impressively linear transduction of angular accelerations. Figure 2, which is taken from Fernandez and Goldberg (1971), shows the response of a unit connected to a semicircular canal in the eighth nerve of a squirrel monkey as the monkey was rocked back and forth in a sinusoidal motion. In the summary of their extensive series of experiments on this system, Fernandez and Goldberg (1971) wrote the following: "In many ways the responses resembled those expected of a linear system. The nonlinear distortion, which mainly reflected asymmetries between excitatory and inhibitory responses, was reasonably low, averaging some 13%" (p. 673). Mountcastle (1967) has proposed the hypothesis that many sensory systems, after what may be an initial nonlinear

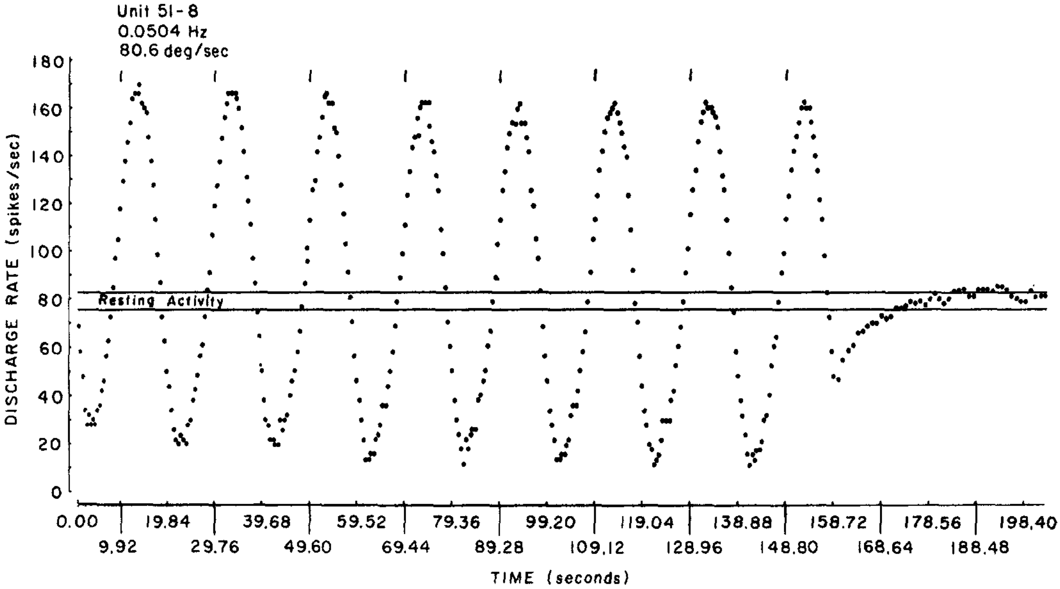

Figure 2. Response of Unit 51-8 (superior canal) to eight cycles of a sinusoidal stimulus at .0504 Hz and 80.6 degrees per second squared. (Stimulus ends at 185.72 sec. Each point represents the average discharge rate for one fortieth of the sine wave cycle [.496 sec]. Vertical marks show instants of peak excitatory acceleration. Lower and upper horizontal lines, respectively, indicate resting discharge before and after stimulation. This is Figure 1 from "Physiology of Peripheral Neurons Innervating Semicircular Canals of the Squirrel Monkey: II. Response to Sinusoidal Stimulation and Dynamics of Peripheral Vestibular System" by Cesar Fernandez and Jay M. Goldberg, *Journal of Neurophysiology*, 1971, *34*, 661–675. Copyright 1971 by the American Physiological Society. Reprinted by permission. Axes relettered for legibility.)

transduction, maintain considerable linearity of coding of some aspects of the input to the highest levels of the nervous system.

We have suggested abrupt limiting in our model. Figure 1 shows one example of this. Other physiological examples are available in several sensory systems. Sometimes limiting is quite abrupt, and sometimes there is a more graded transition region (see, e.g., Maffei & Fiorentini, 1973, Figure 8, republished as Figure 63 in Pöppel et al., 1977; or Creutzfeldt, 1972, Figure 2). To a first approximation, we feel that the exact details of the transition region are not critical. If neurons act like integrators of their inputs, as we suggest, then abrupt limiting or a more gradual transition to limiting will not produce greatly different effects.

As a parenthetical comment, several groups have studied integrator models for various kinds of neuron behavior (Fohlmeister, Poppele, & Purple, 1977; Knight, 1972). Integrator models often, depending on details, show quite good approximations to a linear response to steady inputs over portions of their response range; although detailed behavior is, of course, more complicated than we used for the model presented in our article.

We have made this extended digression into physiology to make the following points: First, limits to nerve cell firing frequency are not those suggested by equilibrium potentials in the simple active cable equation. Second, many cells have a region where they can respond in a simple linear way to their inputs. Third, one sometimes finds rather abrupt limits to the firing rate. We think the neurophysiology gives us some reason for believing that our simplifying approximations of neuron properties are not imposed "by fiat" but do in fact have some justification from the experimental data.

Operation of the Model

Let us briefly discuss some of the aspects of the operation of the model we proposed. Let us stress that we are concerned with the *pattern* of individual activities shown by all the neurons in a set of neurons, which is what leads to study of the state vectors, that is, the set of neuron activities, as primitive entities.

Grossberg (in his section entitled "Positive Eigenvalues Cause Catastrophes in Linear Systems") gives an example of a positive feedback system. However, in this example, there are no cross-terms, that is, where neuron i is connected to neuron j. With only positive values of activity allowed and with no cross-connections, the system in the example must of necessity end with all ones as a final state. As we shall show in a simple example, our model can show richer behavior than this.

Let us first, however, emphasize the need to consider both positive and negative values of cell activity. There are many ways this can be accomplished. Perhaps the simplest is to let the cell be inhibited from a nonzero spontaneous activity level, and let the set of activities correspond to deviations from this spontaneous level. Many physiological examples that look like this can be found. The example (the present Figure 2) given earlier from Fernandez and Goldberg (1971) certainly seems to show this behavior. Here, there is clear transduction around a high spontaneous activity level. High spontaneous rates are found in many eighth nerve units connected to the semicircular canals (Goldberg & Fernandez, 1971). Another means of allowing both positive and negative transduction would be by use of simple circuits of excitatory and inhibitory units as discussed by Kohonen (1977).

We feel strongly that both excitation and inhibition be represented in the activity patterns we are concerned with; by allowing positive and negative values for activity, we formally acknowledge this.

An Example

Some difficulties seem to have arisen over the definition of the word *noise*. Let us give an example of the operation of our system to show both how it can function and what is usually meant by *noise suppression*.

Consider the two-dimensional system shown in Figure 3, which is a system like that considered in the section of our article discussing probability (Anderson et al., 1977) learning. We will assume there are two eigenvectors pointing toward the two corners (1, 1) and (1, −1). Let us construct the system with two different eigenvalues with the ratio 1.33. We can easily construct such a matrix. The two unit vectors corresponding to the corners are

$$\mathbf{e}_A = \frac{1}{\sqrt{2}}\begin{pmatrix} 1 \\ -1 \end{pmatrix}$$

and

$$\mathbf{e}_B = \frac{1}{\sqrt{2}}\begin{pmatrix} 1 \\ 1 \end{pmatrix}.$$

To make the step size small, we chose the eigenvalues to be .04 and .03. To construct the appropriate **A**, then, we have

$$\mathbf{A} = (.04)\left(\frac{1}{2}\right)\begin{pmatrix}1\\-1\end{pmatrix}^{(1,-1)} + (.03)\left(\frac{1}{2}\right)\begin{pmatrix}1\\1\end{pmatrix}^{(1,1)}$$
$$= \begin{pmatrix}.035 & -.005\\ -.005 & .035\end{pmatrix}.$$

A brief check will verify that the corners are in the direction of eigenvectors, and the eigenvalues are correct.

Then consider several starting points, as shown in Figure 3. The trajectories taken by the state vectors after repeated iterations of the form

$$\mathbf{x}(t+1) = (\mathbf{I}+\mathbf{A})\mathbf{x}(t)$$

are shown. The dots are placed every five iterations. Components are limited, so if a component moves out of the boundaries of the square, its component is replaced by that of the square boundary. It can be seen that all starting points within one region end in one corner.

We now have a categorizer of the kind we discussed at length in our article. The output of the system will be one or another corner. Whether or not this is to be considered as "noise amplification" depends on interpretation. If we take as a measure of noise suppression the distance of the desired output activity pattern for a set of inputs from the actual output pattern, the system works quite nicely. The extension of the system to higher dimensions leads to a system with a rich repertoire of categorizations and a complex structure.

A common definition of *noise* refers to perturbations applied to an input. If the system "suppresses noise," then the output is relatively unaffected by some kinds of perturbations of its inputs. Our categorizer is of this type, since as long as an input is not perturbed sufficiently by noise to cross a region boundary, the final state of the system is unchanged. Many strictly linear systems can be shown to suppress noise as well, and a large body of literature in both statistics and communication theory is devoted to this particular problem, which is of great practical interest. Kohonen (1977) has devoted a large portion of his book to discussing the properties of neural models related to those we discussed in our article in the presence of noise.

Connectivity

Nerve cells in most areas of the nervous system have extensive interconnections. Describing in the feedback models how interconnections between neurons in a group of neurons might be developed and their possible uses was the point of the last part of our article (Anderson et al., 1977).

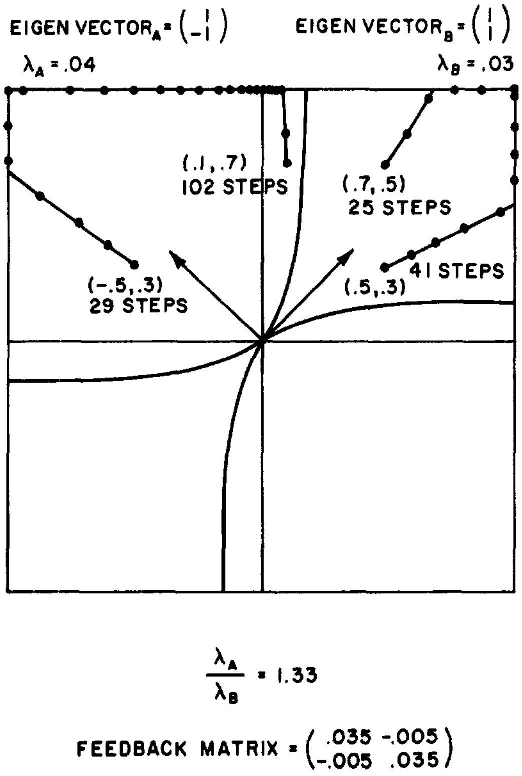

Figure 3. Simple example of a two-dimensional system of the kind proposed in Anderson et al. (1977). (x- and y-axes correspond to activities in a two-neuron system. Feedback is applied through the feedback matrix, which has eigenvectors pointing toward corners and with eigenvalues as shown. Curved lines passing through origin are the boundaries of equivalence regions corresponding to one or another corner. Dots are placed on trajectories every five iterations, and the total number of steps required to reach a corner is placed next to the starting point.)

In our assumptions about the components of state vectors, we were primarily concerned with the richness of coding of events occurring in the inputs to the system (see Cooper, 1974). We assumed that, with respect to the inputs, each individual neuron responded to its own particular set of properties. The initial state vector could potentially start at any point of the n-dimensional space within the box. Connections, developed in the past of the system, then begin to take effect as we have described in the feedback model.

Cortical connectivity is complex and not well understood. The feedback model we presented requires the potential for positive feedback in the sense that the feedback matrix must have positive eigenvalues. This can be accomplished in many ways, but (most reasonably) both lateral excitation and lateral inhibition would be implied. Since an increase in cell firing rate can be accomplished either by direct excitation or by disinhibition (i.e., less inhibition) and a decrease in rate either by direct inhibition or by less excitation, it is hard to draw unambiguous conclusions from neuroanatomy.

There seems to be extensive evidence for lateral inhibition in the cortex. As an anatomical point, excitatory recurrent collaterals of pyramidal cells have been demonstrated (a) in pre-pyriform cortex (Shepherd, 1974, p. 249), (b) in hippocampus (Shepherd, 1974, pp. 271, 273), and (c) in neocortex, where recent results "have indicated the likelihood that pyramidal neurons excite other pyramidal neurons through a direct connection by their recurrent collaterals" (Shepherd, 1974, p. 313). Unraveling degrees, amounts, and kinds of synaptic connections in the neocortex is very difficult; and time, perhaps, will provide the answers.

It seems to be commonly found, however, first, that cortical cells are often highly individualistic in their responses to inputs and, second, that cortical cells on the average over long time periods are often not strongly correlated with each other in the awake, alert animal (see the discussion in Anderson et al., 1977).

Conclusions

We would like to emphasize once more the limited aims of Anderson et al. (1977). We left many questions unanswered and made many simplifying assumptions. As only one example, we did not suggest any way to get an activity pattern out of a corner once it was in one and thus ignored completely the important questions of long-term stability that are of great interest to Grossberg (1978). These questions are important, and we do not wish to suggest otherwise; however, we felt it might be useful to consider a limited model that seemed to give rise to some interesting effects.

We suspect that many nonlinear systems can be constructed to show the multiple stable points of the kind shown by our simple nonlinear system. We used this property to generate the particular simulations we argued were reminiscent of categorical perception and which could also be used as a response selector for probability learning. We suggested the model in the particular form it took because we felt that it was a simple representative of a class of distributed models that arose naturally from one approach to understanding the behavior of activity patterns shown by sets of neurons.

Grossberg's work on nonlinear models, which he reviews in his note, is widely known and respected. In the final paragraph, he mentions that the mechanisms for linear and nonlinear models may be different. However, the experimental data often show regions where linearity is a reasonable approximation. And for many problems, linear models combined with simple nonlinearities may have value for understanding the behavior of complex systems where a more complete analysis fails or is excessively difficult. As long as the limitations and regions of applicability of the approximations one makes are kept in mind, it seems perfectly reasonable to us to investigate simple systems and add complexity as required. The understanding of brain functions poses problems of sufficient magnitude to allow a variety of useful approaches.

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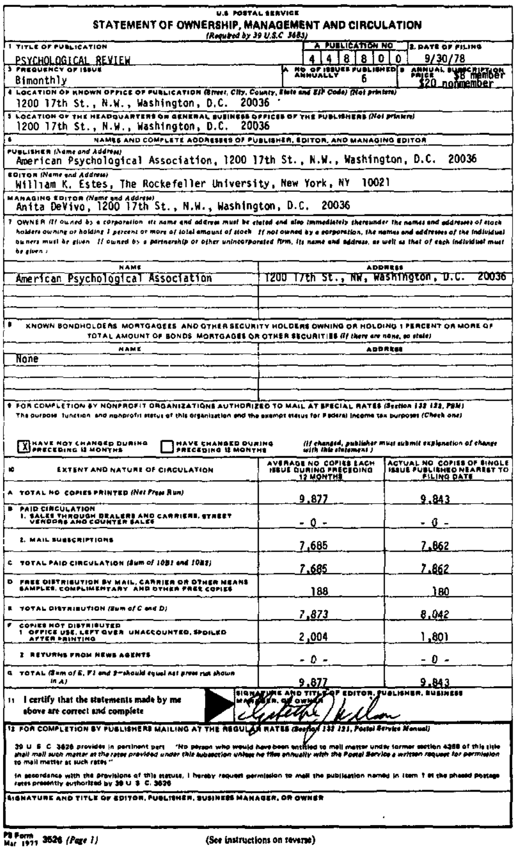

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