Abstract. A model is proposed that is based on certain aspects of sensory cortex. The basic model is a cellular automaton, where the cells represent small groups of neurons in the cortex. All cells are locally interconnected with their three nearest neighbours in each direction, a variable set of weights determines the strength of the connections. The output of the cell is a function of the weighted sum of the inputs. Other variable parameters are the threshold and the number of states. The model is shown to be able to exhibit a wide range of behaviours analogous to the types of behaviour seen in other more general cellular automata. A subset of these behaviour types may be applicable to modelling the functions of sensory cortex.

1. Introduction

Most modelling of the visual system has been done using a hierarchical linear filter approach (e.g. [1]), where each level filters the output from the previous level and thus projects to the next higher level. For the low levels of the visual system this method accurately models many aspects of the processing of visual images. Even at the level of the primary visual cortex this approach has given valuable insight into the processing that occurs. However only about half of all the cells in the primary visual cortex show linear or almost linear responses, the rest have varying degrees of non-linearity.

Primary sensory cortical areas are organized into a regular array of "hypercolumns" [2,3]. Within the hypercolumn there is further subdivision into columnar structure. For instance in the primary visual cortex, each hypercolumn contains orientation and ocular dominance columns. The cellular structure within all columns is basically the same. There are two major features of note in the connections within the cortex (see figure 1). First, most connections, except input and output, are local in nature, extending...
no further than the size of a hypercolumn. Second, many of these connections can be seen as part of feedback loops. The approximate homogeneity of a cortical area and local connections leads naturally to the idea of modelling using cellular automata. Models of this sort have been proposed for the cerebellar cortex [6] and the visual cortex [7]. Cellular automata models assume homogeneity over the entire system and the results show bulk properties of the system being modelled. In contrast to this are various models of parallel processing and learning (some examples may be found in Rumelhart and McLelland [8]) which depend on non-homogeneity and are more concerned with detailed properties of the system. These models may be more applicable to higher cortical regions that do not show the same regularity of structure as the sensory and cerebellar cortices.

Recent advances in the theory of cellular automata [9,10,11], provide the background for the present model. The model is a cellular automaton based on some of the known properties of cortical neurons. A relatively small number of parameters determine the rule governing the behaviour of the model. Using this model I shall examine the various types of behaviour that the system can exhibit and how the various parameters of the model affect that behaviour. Secondly I shall extend the model to include input from outside and an asynchronous mode of calculation, which introduces a more realistic and stochastic element into the system.

2. Model description

A cellular automaton is basically an n-dimensional array, s with elements $s_i$. Each element or “cell” may take on a range of values 0, 1,..., $k - 1$, the
value of the cell being termed its state. The states of cells are changed in
discrete time steps, the array of states at some time $t$ is called a generation.
The next state of a cell depends on the state of a cell and its neighbours.
The rule which determines the next state is the same for all cells. The range
determines the number of neighbours in some direction that can contribute
to the next state. The present model always uses a range $r = 3$.

3. Basic model

The basic model is a cellular automaton where each successive generation is
calculated using a two-step procedure. The first step is to take a weighted
sum of of a cell and its neighbours. A function is then applied to this value
and the result is the value of the cell at the next generation. This procedure
in one dimension is given by the formula:

$$ s_{i+1}^{t+1} = f_p\left(\sum_{j=-3}^{3} w_j s_{i+j}^t\right) $$

(3.1)

where $w$ is the weights vector $(w_{-3}, \ldots, w_3)$.

Similarly in two dimensions:

$$ s_{ij}^{t+1} = f_p\left(\sum_{k=-3}^{3} \sum_{l=-3}^{3} w_{kl} s_{i+k,j+l}^t\right) $$

(3.2)

where $w$ is the weights matrix $[w_{ij}], i, j = \{3, \ldots, 3\}$.

The weights used may be positive or negative.

The functions $f_p$ are based on a difference of logistic functions (see figure 2),

$$ f_p(x) = L_1(x) - \gamma L_2(x) $$

(3.3)

where $L_i$ is the logistic function

$$ L_i = \frac{1}{1 + \exp\left(-\frac{x-x_i}{\rho}\right)} $$

(3.4)

The parameters $x_i$ and $\rho$ are calculated as a function of $k, \theta, w$. The
function $f_p$ is normalized and integerized so that the output is in the correct range $(0, \ldots, k-1)$. Two conditions are necessary in this scheme to
restrict the possible rules to "legal" rules [10]. First, the weights must be
symmetrical, i.e. in one dimension

$$ w_{-i} = w_i $$

(3.5)

or in 2 dimensions

$$ w_{-i-j} = w_{i-j} = w_{-ij} = w_{ij} $$

(3.6)

Second, the functions $f_p$ must satisfy:

$$ f_p(0) = 0. $$

(3.7)

These conditions are satisfied in all cases.
Figure 2: The basic stimulus-response (SR) functions showing the effect of varying $\gamma$. The value of $\gamma$ is shown to the right of each curve.

4. Forcing input

One extension to the basic model described above to apply a constant (time invariant) forcing input. This means that a given cell will receive input not only from itself and its neighbours but some external source as well. The following formula expresses this:

$$a_i^{t+1} = f_p \left( \sum_{j=-3}^{3} w_{ij} s_{i+j}^t + f a_i \right)$$

(4.1)

where $f$ is the forcing weight, $a_i$ is the value of the $i^{th}$ cell of the forcing input.

5. Asynchronous calculation

The basic model uses synchronous calculation to determine the next generation, where the value of all cells are calculated before changing any values. It is also possible to calculate the next generation asynchronously [12]. One way to do this is to choose a number of cells at random and change only their values before continuing. The second extension to the basic model does this, the number of cells to be changed is input as a variable parameter, $A$. With this method of calculation the notion of generation is no longer well-defined. For purposes of display the next generation was arbitrarily defined as occurring after the total number of changes made equalled or exceeded the number of cells.
6. Behaviour of the model

The types of behaviour of the model and the effects of the various parameters on this behaviour are shown in figures 3 through 5. The number of states and the absolute values of the weights have little qualitative effect on the behaviour of the systems. The shape parameter $\gamma$ has its major influence on the temporal behaviour of the system. When $\gamma = 0$ (with a positive center weight) the system tends towards stable states, with the majority of cells taking a value of either 0 or the maximum. As $\gamma$ increases the system goes to oscillatory or chaotic types of behaviour, depending on the weights and the threshold. Systems that converge to stable states generally do so very rapidly (about 5 generations for one-dimensional systems and 10 - 20 for two-dimensional systems).

The weighting function and the threshold have their major influence on the spatial structure of the system. The distribution of excitatory and inhibitory weights affects the spatial structure of the states, e.g. alternating excitatory and inhibitory weights produce a system with alternating zero and non-zero states in each generation. The rate of lateral growth of patterns is determined by both the weights and the threshold. A high threshold or too much side inhibition inhibits lateral spread of patterns. The rate of growth is an important factor in determining whether a pattern will exhibit oscillatory or chaotic behaviour. Class IV like behaviour occurs in the transition region as threshold of a chaotic system is increased (figure 5). In this model Class IV like behaviour appears to occur when the tendency of a pattern to spread laterally is inhibited by a high threshold.

7. Extensions

The major effect of using an asynchronous mode of calculation (figure 6) is on systems that show oscillatory behaviour under synchronous calculation. Strict oscillatory behaviour is dependent on synchronous calculation. Other types of behaviour are affected to a much smaller degree although the rate of convergence is somewhat slower. The effect of applying a forcing input (figure 7) is to entrain the system to the forcing input, although the behaviour is not significantly affected otherwise. The behaviour of one-dimensional systems (figure 8) is not qualitatively different, except that oscillatory behaviour appears to be less common, given the general form of the weighting functions I have been using.

8. Discussion

The relation of the model to cortical physiology occurs at two basic levels. First, the model was constructed based on certain aspects of the nervous system. Second, the behaviour of the model should correspond to the behaviour of the nervous system for appropriate values of the parameters.
Figure 3: The effects of varying $\gamma$ and the threshold, $\theta$, are shown for a sample of different weighting functions. For a given set of weights increasing $\gamma$ leads to either oscillatory or chaotic behaviour. Increasing threshold (from top to bottom in the figures) generally reduces the number of active sites. All systems started from a random initial configuration and had the number of possible states, $k = 8$. 
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Figure 4: The behavior of some systems starting from non-random initial conditions. Parts 4.2 - 4.4 also show the effect of adding noise to the initial configuration. The noise level in parts 4.2 and 4.3 is a change of ±1 state value in about half of the sites. In part 4.4 a single site near the center was changed and the disturbance can be seen propagating out from this region.
Figure 5: The effect of increasing threshold on a chaotic system. The system passes through a region where Class IV-like behaviour is observed.
Figure 6: The effect of asynchronous calculation on the behaviour of the systems. The systems shown correspond to stable, oscillatory, chaotic and Class IV-like respectively. Compare these with figures 3.1, 3.3, 5.1 and 5.2.
Figure 7: The addition of a forcing input to the model. The forcing input is shown as a single line below each system. All initial configurations were random.
Figure 8: Some examples of two-dimensional systems. The configurations shown are either the final (stable) state or the one-hundredth generation. A cross-section through the centre of the system is also shown beside the final configuration. The weights matrix $A$ used are shown here.
8.1 Physiological basis of the model

The basic elements of the model are the cells of the array which constitute the cellular automaton. The correspondence of these cells is not necessarily one-to-one with neurons in the nervous system. The cellular automaton cells may be considered rather to correspond with a small group of neurons (module) within a hypercolumn of the cortex. For example, the module may correspond to a group of cells such as those shown in the basic circuit diagram in figure 1.

Most neurons require a minimum level of input before they fire; this is called the threshold. A second effect of threshold is to shift the stimulus-response curve to higher values, this effect was incorporated into the present model. The weights represent the strength of the connections between neighbouring modules. These weights are assumed to be the same for all modules and to be relatively constant on a short time scale. Changes in the weights over long time scales may be, at least in part, a basis for learning.

The stimulus-response function represents the input-output relations of this module. In the case where the SR function is based on the logistic curve ($\gamma = 0$), the module may represent a single neuron or a group of similar neurons. This type of curve is seen at different levels of the nervous system, from the level of the synapse [13], to the level of psychophysics which represents the functioning of many parts of the brain [14]. However, the peaked SR functions ($\gamma > 0$) are unlikely to implemented in a single type of neuron and may correspond to the interactions of both excitatory and inhibitory neurons. For example the sum of an excitatory neuron and a higher threshold inhibitory neuron could produce these types of SR functions.

The extensions to the basic model were designed to produce a more realistic model of the cortex. The basic model in 2-dimensions corresponds to a sheet of cortical tissue, however, the cortex does not exist as an isolated sheet. The input to a region of the cortex may come from a distant region, e.g. input to the visual cortex comes from the lateral geniculate nucleus. The addition of a forcing function to the model is intended to simulate this input, although the restriction to time invariant input is itself a simplification. The extension to asynchronous mode of calculation was introduced because the cortex, unlike a computer, does not have a single clock controlling all cells. The method of asynchronous calculation used here also introduces a stochastic element into the model.

8.2 Relation of the model with physiology

I have tried to to show that this model has a reasonable basis in known physiology, but the acid test of any model is whether or not it can predict the behaviour of the system being modelled. Unfortunately, at the present state of technology the measurement of the individual states of a large group of neurons is impossible. Nevertheless, some general observations can be made.
Systems that have a high threshold or weights with outside inhibition tend to produce localized structures. The excitation of a region of space does not propagate to distant regions, this is also true of cortical regions under normal conditions. Under certain pathological conditions (e.g. epilepsy, hallucinations) this is no longer true and uncontrolled spread of excitation is observed. Reduction or elimination of the inhibitory portions of the weights appears to produce just this kind of behaviour. Ermentrout and Cowan [15] have proposed a model of visual hallucinations where the triggering instability is decreased inhibition and increased excitation. Babloyantz, Salazar and Nicolis [16] have shown that EEG measurements of the brain under various conditions give different values for the dimension of the underlying dynamics. In particular the arousal state of the organism affects the dimensionality. Increasing threshold reduces the excitability of the cells and reduces the entropy or dimensionality.

The control of threshold and the ratio of excitation to inhibition could occur in at least two different manners in the nervous system. First, there are a number of non-specific fibres originating in the brain stem and terminating in a relatively large region of cortex. These fibres may be used to change the parameters of cells in a given region of cortex or the entire cortex. Second, there are various chemical factors called neuromodulators that can react with receptors on the cells’ surface and change their behaviour.

Systems that use a simple logistic based SR function tend to stabilize very quickly. The final stable states can be compared to point attractors in some phase space. The basin of attraction consists of those initial configurations that closely resemble one another. These types of systems seem to provide a better model of the normal functions of the brain in that the systems are resistant to noise and will produce an output that is related to the input. Chaotic and Class IV systems are, by definition, sensitive to the initial conditions (input).

9. Conclusions

Cortical physiology provides the basic parameters used to construct the model presented here. The model is not intended to accurately model any real nervous system, but rather to examine overall properties of a connected group of discrete neuron-like elements. A relatively small number of parameters, similar to those that might be found in a nervous system, is used to determine the rule used by the model. Despite the fact that this model is more restricted in its rules than many cellular automata, where an output state can be assigned to each individual input configuration, it can nevertheless exhibit a wide range of behaviour as the parameters are varied. Some types of behaviour may be applicable to cortical function, for example the localization of excitation and the compression of information that occur in the systems showing stabilizing behaviour.
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References


