Learning by Selection in the Trion Model of Cortical Organization

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The basic issue of whether mammalian learning in cortex proceeds via a selection principle, as stressed by Edelman, versus an instructional one is of major importance. We present here a realization of selection learning in the trion model, which is based on the Mountcastle columnar organizational principle of cortex. We suggest that mammalian cortex starts out with an a priori connectivity between minicolumns that is highly structured in time and in space, competing between excitation and inhibition. This provides a "naive" repertoire of spatial-temporal firing patterns that stimuli and internal processing map onto. These patterns can be learned with small modifications to the connectivity strengths determined by a Hebbian learning rule. As various patterns are learned, the repertoire changes somewhat in order to respond properly to various stimuli, but the majority of all possible stimuli still map onto spatial-temporal firing patterns of the original repertoire. In order to show that the example presented here is showing true selectivity and is not an artifact of more stimuli evolving into the learned pattern, we develop a selectivity measure. We suggest that some form of instructional learning (in which connectivities are finely tuned) is present for these difficult tasks requiring many trials, whereas the very rapid learning involves selectional learning. In contrast, finely controlled motor movements requiring a high precision of accuracy need many trials of learning to accomplish this, and may use an instructive learning method that involves fine tuning the connectivity.

We do not enter the debate (Crick, 1989, 1990; Michod, 1990; Reeke, 1990) concerning Edelman's proposed neuronal group realization of the selection principle of learning, but we present here a realization of selectional learning in the trion model of the cortex, which is highly structured (Shaw et al., 1985, 1988; Silverman et al., 1986; Leng and Shaw, 1991; McGrann et al., 1991; Leng et al., 1992, 1993). With a selection principle, the various responses of the network exist prior to any stimuli and constitute the naive repertoire. The stimuli "selects" out a particular response from the naive repertoire. This selection process takes place, in the trion model, with small changes in the connectivity through a Hebbian (Hebb, 1949) learning algorithm. This learning should proceed very rapidly since the response is already built in and doesn't have to be created from repeated exposure to the stimuli as in an instructional principle. In general, different stimuli should select out different responses, although some may select out the same response, indicating some similarity between the two stimuli. Also, the response should not be overlearned to the point that all stimuli select out the same response. We will discuss the qualitative differences between a highly structured connectivity, which we use in the trion model, versus an initial set of random connections.
Hgnra 1. A schematic description of Edelman's basic idea of learning by selection. Initially, there is a repertoire of cortical responses $\{R_i\}$ present at birth so that a given stimuli $S_i$ might excite a number of these inherent responses. After learning, or through experience, $S_i$ will lead mainly to just one of these responses, $R_i$.

Mountcastle (1978) proposed that the cortical column (Goldman-Rakic, 1984) is the basic network in the cortex and is composed of small irreducible processing units called minicolumns (see Fig. 2; we note that the beautiful optical recording results by Bonhoeffer and Grinvald, 1991, in secondary visual cortex show a truly striking similarity to the cartoon-idealized primary visual cortex shown here). Such a column has the capability of being excited into complex spatial-temporal firing patterns (for further discussion of the cooperativity involved in the functioning of small groups of neurons, see Shaw et al., 1982). The assumption is that higher mammalian processes involve the creation and transformation of such complex spatial-temporal firing patterns (in contrast to a "code" that involves sets of neurons firing with high frequency). Evidence is accumulating that this spatial-temporal code describes the "internal language" of the cortex (Eckhorn et al., 1988; Gray and Singer, 1989; Gray et al., 1989; Dinse et al., 1990; Richmond et al., 1990; Singer, 1990; Leng et al., 1993; Shaw et al., 1993).

The trion model of the cortical column (Shaw et al., 1985, 1986; Leng and Shaw, 1991; McGrann et al., 1991) is a mathematical realization of Mountcastle's organizational principle. A trion (Fig. 3) represents an idealized minicolumn or roughly 100 neurons, and has three levels of firing activity: above average, average, and below average. The "naive" (before learning) interactions among the trions in the column are taken to be localized, highly structured, and competing (excitatory and inhibitory). The firing state of the network (cortical column) of trions is updated in a manner related to the states of the previous two time steps (Fig. 4). A column with a small number of trions having structured connections yields a large repertoire of quasi-stable, periodic spatial-temporal firing patterns, defined as magic patterns, or MPs, which can be excited. These inherent patterns are called "magic patterns" because of their ability to be learned or enhanced via a Hebb learning rule to a large cycling probability. The repertoire of periodic MPs is found by evolving all possible initial states (of the first two time steps) by following the most probable or deterministic path. In a full probabilistic (or Monte Carlo) evolution, the MPs evolve in natural sequences from one to another. It has been shown that the probability of each MP remaining in that pattern can be enhanced by only a small change in connection strengths using a Hebbian learning rule (it is not our purpose here to examine fully the assumptions of the trion; see Leng et al., 1992, for a suggested test of the trion model with large clinical significance). We demonstrate here the selectional learning properties of the trion model in a (typical) simple example. In order to show that the example presented here is showing true selectivity and is not an artifact of more stimuli evolving into the learned pattern, we develop a selectivity measure. It is the repertoire of MPs that will be the repertoire of responses in our realization of the Edelman selection principle shown in Figure 1. This repertoire arises from the structured nature of the cortex.

Materials and Methods

Basic Model

In brief, the trion model was developed starting from Little's (1974; Little and Shaw, 1978) neural network
analogy to the Ising spin system, and modified in a direction inspired by Mountcastle's (1978) organizational principle (Fig. 2) and by the striking physical spin model results of Fisher and Selke (1980). The trion represents the minicolumn and has three levels of firing activity. Following Fisher and Selke, the interactions among the trions are taken to be localized, competing (between excitation and inhibition), and highly structured. The firing state of the network (cortical column) of N trions is updated in a probabilistic way related to the states of the two previous time steps as in Figure 4. The probability $P(S) = g(S) \exp(BM,S)$ of the $i$th trion having a firing level or state $S_i = 1, 0, -1$ at time $n\tau$ is given by

$$P(S) = \frac{g(S)\exp(BM,S)}{\Sigma g(S)\exp(BM,S)},$$  

where $S_i$ and $S_j$ are the states of $j$th trion at the two earlier times $(n-1)\tau$ and $(n-2)\tau$, respectively. $V_i$ is an effective firing threshold. The three possible firing states (of each trion) denoted by $+, 0, -$ for $S = 1, 0, -1$ represent, respectively, a large “burst” of above average firing, an average burst, and below average firing. The term $g(S)$ with $g(0) \triangleright g(\pm)$ takes into account the number of equivalent firing configurations of the trion’s internal neuronal constituents. [E.g., in a trion representing a group of 90 neurons, firing levels of $+, 0, -$ could correspond to 90–61, 60–31, 30–0 neurons firing, respectively. There are many more combinatorial ways of generating the 60–31 level (Roney and Shaw, 1980; Shaw et al., 1982). This feature, $g(0) \triangleright g(\pm) = g(-)$, gives stability to the trion model firing patterns.] The fluctuation parameter $B$ is inversely proportional to the noise, and results (Shaw and Vasudevan, 1974) from the statistical nature of neurotransmitter release from the synapses (Katz, 1969). Studies of the trion model for memory (Shaw et al., 1992) and for pattern recognition (McGrann et al., 1989; McGrann, 1992) have been reported. Basically, the success of these studies is due to the fact that the localized, competing (between excitation and inhibition), and highly symmetric connections yield a huge repertoire of inherent quasi-stable, periodic firing patterns, MPs. Further, these MPs evolve in certain natural sequences from one to another (see, e.g., Fig. 1 of Shaw et al., 1985) in Monte Carlo simulations (described below). Any of the MPs can be readily learned or enhanced with only small changes in the interaction strengths using the Hebb learning algorithm:

$$\Delta V_{ij} = \epsilon \sum_{n} S_i(n\tau)S_j((n-1)\tau),$$  

$$\Delta W_{ij} = \epsilon \sum_{n} S_i(n\tau)S_j((n-2)\tau), \quad \epsilon > 0,$$

where $n$ runs over the time steps in one cycle of the MP. Simply extending this learning rule to a third time step [using the correlation $S_i(n\tau)S_j((n-3)\tau)$] significantly enhances the effects of learning with a smaller change in the total connectivity (Leng, 1990; McGrann, 1992). We use this three-time-step version of the Hebb learning rule (Eq. 2) in the calculations presented in this article. One possible physiological origin for a dependence on the previous (three) time steps involves the circulation of activity through the cortical layers (Krone et al., 1986; Shaw et al., 1993).

Let us define the cycling probability $P_c$(MP) that the firing pattern for the columnar trion network remains in the MP for one cycle of the repeating MP. The $P_c$(MP) is calculated by multiplying the probabilities $P(S)$ (Eq. 1) of each trion $i$ being in the state $S$ at time $n\tau$, given by that MP for its whole cycle length:

$$P_c(MP) = \Pi_i P(S_i(n\tau)),$$

where $i$ runs over the $N$ trions in the columnar network. As a result of learning an MP using the Hebb algorithm (Eq. 2), the cycling probability $P_c$(MP) (Eq. 3) is increased. Further, after learning, many more initial states, as noted below, will go to the learned MP (and some related MPs). Note that these MPs evolve in natural sequences (see below) from one to another in a Monte Carlo probabilistic calculation described below.

**Monte Carlo Simulations**

As described in the introductory remarks, the trion model represents a mathematical realization of the Mountcastle organizational principle for the cortical column as the basic neuronal network in the cortex. Here we explicitly describe the simulations giving the (probabilistic) Monte Carlo evolutions of spatial-temporal firing patterns of a trion network.

1. We specify the parameters of the trion network: the number of trions $N$, the degeneracy factors $g(S)$, the connectivities $V_{ij}$ and $W_{ij}$, the firing...
Figure 4. One network of trions at three time steps, showing the firing states $S$ and the connections $V$ and $W$. For $N$ trions in the columnar network, we have the ring-like connections trion $i = $ trion $i + N$, as in Figure 2.

Figure 5. Roulette analogy for a Monte Carlo evolution. The probabilities $P(S), P(+), P(-)$ calculated in item 3 add up to 1.0 and can be represented by three segments or bins of total length 1.0 with the individual lengths being these specific values $P(S)$ arranged in a specific order. For example, let $P(-) = 0.2$, $P(0) = 0.5$, and $P(+) = 0.3$ so that we have probability segments 0.0-0.2 for $S = -1$, 0.2-0.7 for $S = 0$, and 0.7-1.0 for $S = 1$. Then, a random number between 0.0 and 1.0 is chosen by the computer and thus the segment that the random number falls into determines the $S$ to be chosen. This is a standard Monte Carlo simulation technique as illustrated in Figure 5. This procedure is done for each of the $N = 6$ trions to determine the pattern at that time step. Then continue to repeat items 3 and 4.

Figure 6. A choice for the firing states for the initial two times steps is made. Since each of the six trions in each time step has three possible firing levels $S$, there are $3^6 = 531,441$ possible choices. Note that each trion is distinguishable.

(2) A choice for the firing states for the initial two times steps is made. Since each of the six trions in each time step has three possible firing levels $S$, there are $3^6 = 531,441$ possible choices. Note that each trion is distinguishable.

(3) Given the firing states for each trion at the two earlier times $(n - 1)\tau$ and $(n - 2)\tau$, the probability $P(S)$ for the $i$th trion being in state $S$ at time $n\tau$ is calculated from Equation 1.

(4) The three probabilities $P(0)^-, P(+), P(-)$ calculated in item 3 add up to 1.0 and can be represented by three segments or bins of total length 1.0 with the individual lengths being these specific values $P(S)$ arranged in a specific order. For example, let $P(-) = 0.2$, $P(0) = 0.5$, and $P(+) = 0.3$ so that we have probability segments 0.0-0.2 for $S = -1$, 0.2-0.7 for $S = 0$, and 0.7-1.0 for $S = 1$. Then, a random number between 0.0 and 1.0 is chosen by the computer and thus the segment that the random number falls into determines the $S$ to be chosen. This is a standard Monte Carlo simulation technique as illustrated in Figure 5. This procedure is done for each of the $N = 6$ trions to determine the pattern at that time step. Then continue to repeat items 3 and 4.

Repertoire of MPs and Learning of an MP

Having made the choice of parameters in item 1 above, the repertoire of MPs or inherent, quasi-stable, periodic firing patterns is found as follows. For a given initial firing state (item 2), follow the procedure of always choosing the $S$ for each trion that has the largest probability $P(S)$ instead of using the Monte Carlo rule (item 4). In the above example, the $S$ would be 0.] The time evolution rapidly goes into a repeating spatial-temporal pattern or MP. (This type of calculation allows one easily to test whether an arbitrary spatial-temporal pattern is an MP.) Going through all possible initial states (item 2) gives all the MPs (the repertoire of MPs). An MP has the property of being readily learned or enhanced using the three-time-step version (described above) of the Hebbian learning rule (Eq. 2) with only a small change in the connections; that is, only a small value of $\epsilon$ is needed. These small changes in the connections give only a small change in the repertoire of MPs. After learning, when
Figure 8. The initial repertoire of MPs for the connectivity given by Equation 4 is found by deterministically (see Materials and Methods) evolving all possible $3^2$ initial states until repeating patterns, the MPs, are obtained. Each square represents a neuron with three levels of firing activity: above background (white), background (gray), and below background (black). Each horizontal row represents a ring of interconnected (as in Fig. 3) neurons (so that the sixth square wraps around to the first) and time evolves downward. There are a total of 155 MPs that can be completely classified by their distinct spatial rotations into 34 groups of MPs shown here. The group number is listed on the top left corner, while the number of MPs in each group is given in braces (cyclically rotate the MP so that the first column is the second, etc.: if the MP is not a temporal rotation of any of the other elements in the group it is considered distinct). In a Monte Carlo calculation (see Materials and Methods) these MPs would flow from one to another.
a Monte Carlo calculation is done, the evolution will both go to the learned MP (and some related MPs) more often, and remain in it longer. Furthermore, an arbitrary spatial-temporal pattern cannot be readily learned; only an MP can be learned to a high $P_c$ (Leng, 1990; McGrann, 1992).

**Learning for Structured versus Random Connections**

Let us examine a specific example of the repertoire of MPs for structured connections in an $N=6$ network. Consider the connectivities and other parameters in Equation 1 to be as follows:

$$V_u = 2, \quad V_{i+1} = V_{i-1} = 1, \quad W_v = -V_v$$

with thresholds $V_i = 0$, all other $V_v$ equal to 0, $g(0)/g(\pm) = 500$, and $B = 6.3$ (the connections, Eq. 4, fall off spatially; temporally we know that postsynaptic inhibition has a slower time course, leading to a negative $W$). Then, following the calculations in the section above, each of the $3^{12} = 531,441$ possible choices for the initial states is followed to find the 155 MPs shown in Figure 6 with an average recall time $\tau$ of 3.5t (McGrann et al., 1991) (note that all the MPs in Fig. 6 have cycle length 6 except for MP 33, which has cycle length 1; this is related to the specific choice of connections, Eq. 4, and not the number of trions; for other examples, see Shaw et al., 1985; Silverman et al., 1986). These 155 MPs can be placed into 34 sets as shown in Figure 6, where the MPs in a set are related to each other by a spatial rotation among trions, $R$, among the (distinguishable) trions (Silverman et al., 1986). Other symmetries among these MPs can be used to categorize groups of MPs (McGrann, 1992).

Consider now learning an MP from Figure 6 using the Hebb learning algorithm, Equation 2. The example of learning MP 1(0) [where the (0) denotes the MP obtained from the MP 1 specifically shown in Fig. 6, by operating 0 times with spatial rotation operator $R_I$] is shown in Figure 7, where we plot the probability of cycling $P_c$ (as defined in Eq. 3) versus $\epsilon$. Note that as a result of learning this MP 1(0), the connections in Equation 4 will be modified according to Equation 2. For example, here, $V_{i+1} = 1$ and $V_{i-1} = 1 + 2\epsilon$, so we say that the precise symmetry, $V_{i+1} = V_{i-1} = 1$, is slightly broken by learning for small $\epsilon$.

To contrast these results for our highly structured connections (Eq. 4), we choose several sets of random connections. In general, three qualitative features stand out in comparing structured connections versus random connections (McGrann, 1992): (1) the repertoire for the random connections has a much smaller MP than for the structured connections, (2) the average recall time $\tau_w$ is much larger for the random connections than for the structured connections, and (3) the learning properties of an MP (of comparable cycle length) are largely reduced for the random connections as compared to the structured connections.

**Results**

A selection theory of learning inherently contains a "naive" or preexisting repertoire of responses to stimuli as in Figure 1. For our trion model, this repertoire of responses is the repertoire of MPs determined by the procedure given in Materials and Methods. When external stimuli are internally processed, these events map onto MPs based on the properties of the stimuli. The number and type of MPs in the naive repertoire depend on the connections. A crucial feature as stressed in the previous section is that structured connectivity is necessary for the existence of a large repertoire of MPs. We have suggested that there is increasing evidence for such structure (Leng and Shaw, 1991; Leng et al., 1993). These interactions (Fig. 4) among the trions in a column are taken to be localized, highly structured, and competing between excitation and inhibition. For our example, we choose these "naive" (nonzero) connections to be the simple values given in Equation 4 that fall off spatially; temporally we expect that postsynaptic inhibition has a slower time course. (These connections are not unique and the brain probably utilizes different sets depending upon the processing tasks of the area of cortex where it is located.)

The repertoire is found from deterministically evolving all $3^{12}$ possible initial firing states as described in Materials and Methods. There are 155 distinct MPs (temporal rotations of an MP are not distinct). If the 155 MPs are grouped according to their qualitative features, there are 34 groups that result, as can be seen in Figure 6. These are the inherent natural firing patterns of the network that would comprise the types of responses of the network before learning.

For our simple, typical example, consider a particular external stimulus that then results in the excitation of a trion network. In particular, we imagine that our stimulus excites part of the first two time steps as in Figure 8. The three "unspecified" trions in Figure 8 (giving 27 possibilities) denoted by diagonal stripes might represent various backgrounds. For example, the stimulus might be a rhino while the background might be a zoo, a plain in Africa, or shopping
Figure 8. The stimulus plus background states chosen to illustrate the selection principle in the trial model is given at the top, where the three diagonally striped squares are varied for the 27 possible combinations. Each stimulus plus background state is discriminantly evolved (see Materials and Methods) until it reaches an MP. Initially the "naive" 27 stimulus–background pairs evolve into a subrepertoire of 16 different MPs, which are shown here on the left as 10 distinct groups in a format similar to Figure 6. The first number is the group number, while the different spatial rotations (0 = unrotated MP, 1 = one rotation to the right...) are listed in the parentheses. After learning MP 1(0) with a learning coefficient of $\epsilon = 0.025$ given in Equation 2, the stimulus–background pairs discriminantly evolve into a subrepertoire of eight MPs shown on the right. Before learning four stimulus–background pairs evolve into MP 1(0), while after learning 12 pairs evolve into it.
The 27 different initial stimulus–background states at the top of the figure were evolved deterministically until an MP was found. Before learning, this lead to a subrepertoire of 16 MPs that are shown at the left of Figure 8.

Consider that the rhino in its background surroundings initially excited MP 1(0). This choice is arbitrary. The assumption is that once this particular MP has been excited (by the rhino plus a particular background) it is enhanced through the Hebb learning rule. Then, using our three-time-step version (Leng, 1990; McGrann, 1992) of the Hebbian learning rule (Eq. 2), the “naive” connections (Eq. 4) were modified. In Figure 7, \( P_c \) versus the learning coefficient is graphed showing the increase in probability as the MP 1(0) as a function of the learning coefficient \( \epsilon \).

The probabilistic evolution of the 27 initial stimulus–background states was performed 500 times each. Without learning, only 1% of these 13,500 trials evolved into MP 1(0). As the learning coefficient increased, the number of stimulus–background pairs that recalled or evolved into MP 1(0) increased to roughly 30% (see Fig. 9). The results of the Monte Carlo calculations (with MPs grouped along with their spatial rotations as in Fig. 6) for no learning and for learning with a learning coefficient \( \epsilon = 0.025 \) are shown in Figure 10. Only those MP groups recalled by greater than 1% of the stimulus–background pairs are shown in Figure 10. Notice that the MP groups 2, 3, and 12 correspondingly increase their respective recall percentages after learning MP 1(0), thereby forming a category of MPs that are likewise enhanced.

In order to show that the example presented here is showing true selectivity and is not an artifact of more stimuli recalling or evolving into MP 1(0), we develop a general selectivity measure. Let

\[
\text{sb} = \text{stimulus–background states} \\
\text{n}_{\text{sb}} = \text{number of sb pairs} \\
\text{n}_{\text{si}} = \text{number of sb pairs evolving into learned MP} \\
\text{n}_{\text{so}} = \text{number of sb pairs evolving into learned MP before learning} \\
\text{N}_{\text{a}} = \text{total number of all initial states} = 2^{12} = 531,441 \\
\text{N}_{\text{d}} = \text{all initial states that evolve into learned MP} \\
\text{N}_{\text{b}} = \text{all initial states that evolve into learned MP before learning} \\
\text{A}_{\text{b},} = \text{total number of all initial states} = 2^{12} = 531,441, \\
\text{N}_{\text{b}} = \text{all initial states that evolve into learned MP} \\
\text{N}_{\text{d}} = \text{all initial states that evolve into learned MP before learning}.
\]

Then, our selectivity ratio \( S_e \) is defined as

\[
S_e = \left[ \frac{(n_{\text{si}} - n_{\text{so}})/n_{\text{so}}}{(N_{\text{d}} - N_{\text{b}})/N_{\text{a}}} \right]. \tag{5}
\]

\( S_e > 1 \) then is required for selectivity. In contrast, \( S_e < 1 \) would indicate a general increase in the number of initial states evolving into the learned MP.

Before learning, there were 155 MPs in the repertoire found from the deterministic evolution of all possible 531,441 initial states of which \( N_{\text{a}}/N = 3.0\% \) that recalled or evolved into MP 1(0). After learning MP 1(0) with a learning coefficient of 0.025, there were 88 MPs and \( N_{\text{d}}/N = 9.3\% \) of the initial states evolved into MP 1(0). The deterministic evolution of the \( n_{\text{so}} = 27 \) stimulus–background pairs into MP 1(0) changed from \( n_{\text{so}} = 4 \) \( n_{\text{so}}/n_{\text{d}} = 14.8\% \) before learning to \( n_{\text{so}} = 12 \) \( n_{\text{so}}/n_{\text{d}} = 44.4\% \) after learning. From Equation 5, then, \( S_e = 4.7 \). Selectivity is thus demonstrated. (This was also true for smaller \( \epsilon \).

The example of selective learning shown here is just one of several such cases that were examined (McGrann, 1992).

**Discussion**

We have demonstrated (by presenting a simple, typical example) that the trion model of cortical orga-

![Figure 8. Percentage recall versus \( \epsilon \) for MP 1(0). A Monte Carlo calculation for each of the 27 stimulus-background pairs was performed 500 times per \( \epsilon \). The percentage of Monte Carlo calculations (or percentage recall) that evolved into MP 1(0) was determined for different amounts of learning, ranging from \( \epsilon = 0 \) (no learning) to \( \epsilon = 0.025 \). Notice that even though there was only a small change in connectivity, the percentage recall changes from less than 1% to about 30%.

![Figure 10. The percentage recall (as described in Fig. 9) is shown here before and after learning (\( \epsilon = 0.025 \)) MP 1(0) for each group given in Figure 8 that had a percentage recall greater than 1%. (Note that the MPs 6(5), 7(3), and 15(5) in Fig. 8 do not fulfill this criterion.) Before learning, the stimulus-background pairs probabilistically evolve into MP 0 the most, while after learning, MP 1(0) becomes the dominant MP. Groups 2, 3, and 12 correspondingly increase their respective recall percentages after learning MP 1(0), thereby forming a category of MPs that are likewise enhanced.)
nization gives a realization of the Edelman selection principle of learning (Fig. 1). However, in contrast to the Edelman realization via the neuronal group selection, the trion model has a very large naive repertoire of quasi-stable spatial temporal firing patterns, MPs, any of which can be selected out through the Hebbian learning rule (Eq. 2). As we saw in Figure 10, only a small modification of synaptic connections among the trions, \( e = 0.025 \), was necessary to select out an MP and yield it as the dominant response. Further, we defined, above, the selectivity ratio \( S_K \) (Eq. 5), which gives a quantitative measure of the true nature of the selective change after learning, and showed that our example clearly satisfied this criterion.

After learning an MP with a relatively small \( e \) (<0.025), the exact symmetry in the "naive" connections (Eq. 4) is broken, leading to a loss in the number of MPs from the naive repertoire (before learning) to the new repertoire (after learning) as found in the deterministic (most probable) calculations. However, when the Monte Carlo (full probabilistic) calculations are done, these "lost" MPs will reappear and can be learned with the Hebb rule, bringing them back to the (deterministic) repertoire. Thus, we might introduce the concept of the actual or dynamic repertoire (McGrann, 1992).

To appreciate the possible huge size of the trion model repertoires for even these small six trion networks, we note that the (nonzero) connections \( V_{u+1} = 1.0, V_{u+1} = 1.0, W_{u+2} = -1.0, W_{u+2} = -1.0 \) gave 1804 MPs (see Table 1 of Shaw et al., 1985). As the number of trions in the cortical column increases, the size of the repertoire increases (nonlinearly). We expect that a more realistic cortical column would have perhaps as many as 20 minicolumns or trions. Furthermore, as we couple several columns together (Leng and Shaw, 1991; Leng et al., 1993), again the repertoire increases. The importance of the symmetry of the connections and of the competition between excitation and inhibition is illustrated in McGrann et al. (1991): 20% changes from the connections in Equation 3 decrease the number of MPs by only a factor of two, illustrating the robustness of the model. However, a random set of connections can decrease the number of MPs in a repertoire by two orders of magnitude! Furthermore, the recall time (the number of time steps, on the average, for an initial state to project onto an MP) for an MP is considerably faster when the connections are structured versus random.

Clearly, we have presented only a simple realization of the Edelman selection theory of learning in the example in this article. Any memory trace of a higher level response would involve many cortical columns and several cortical areas. This, in fact, should considerably enhance the quantitative nature of our results in the manner emphasized by von Neumann (1956) in his classic report on building reliable organisms from components with errors in their performance. The high symmetry of the Mountcastle columnar organizational principle, and the additional assumptions in the trion model based on it are clearly huge simplifications. However, we believe the power and robustness of the trion model make it useful to consider advantages of some generalized, more realistic versions of it. Thus, for example, we suggest that the arguments (Swindale, 1990) over whether all minicolumns or all columns need to have the same number of neurons are irrelevant for understanding the dynamics involved in the Mountcastle columnar organizational principle. We propose that there will be these more biological realizations having structured (in space and time), competing connections among groups of neurons leading to large repertoires of inherent spatial temporal patterns that can be readily learned. These repertoires then will serve as the basis of implementing the Edelman selection principle. It is apparent that as neuroanatomical and neurophysiological techniques have improved in the past decade, more and more structure has been found in the cortex. We expect this trend to continue (Leng and Shaw, 1991; Leng et al., 1993). This in turn makes our example presented here more relevant in understanding the existence of a selective-type learning capability in the cortex.

In conclusion, we stress that the conceptual distinction between a selectional theory of learning in cortex and an instructional one is of major importance. Selectional learning can proceed much more rapidly than instructional learning, and with comparatively small changes in connectivity. One-trial learning would be very hard to understand in an instructional neuronal network model. We suggest that some form of instructional learning (in which connectivities are finely tuned) is present for difficult tasks requiring many trials, whereas very rapid learning involves selectional learning. Both types of learning are crucial in understanding behavior.

Notes
This research was supported in part by the REU program of the National Science Foundation and by the National Association of Music Merchants. K.V.S. was supported in part by a University of California Presidential Undergraduate Fellowship. We thank one of the anonymous referees for very useful comments.

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