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Associative Recall Properties of the Trion Model of Cortical Organization

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Abstract. We developed a cooperative model of the cortical column incorporating an idealized subunit, the trion (which represents a localized group of neurons), and a discrete time step for firing. We found that networks composed of a small number of trions (with symmetric interactions) supported up to thousands of quasi-stable, periodic firing patterns (MPs) which could be selected out with only small changes in interaction strengths using a Hebb-type algorithm. Here we report a study of the associative recall properties showing striking features: By considering all possible initial firing patterns (for a given set of network connections), we find 1) It takes on the average only 2–5 time steps to recall an MP. 2) Many of the MPs can be individually accessed by thousands of different initial patterns. The variety of examples presented illustrate the rich, general nature of the model.

One of the most important problems in the theoretical studies of memory is to investigate the retrieval of information. [See, e.g., (Hinton and Anderson 1981) and the references in the review article (Kohonen et al. 1981).] The associative recall properties of any neuronal memory model are of paramount interest. Although a particular model might be able to encode or store many "pieces of information" we believe that two crucial properties of associative retrieval should also be present: 1) Rapid recall of the information and 2) access of the information from *many* different stimuli. Both of these properties are present in human memory retrieval as contrasted to the *usual* retrieval of information in the digital computer. (Unless specially programmed, the recall of information in the computer is 1) searched for serially and 2) accessed via very specific cues.) The purpose of this paper is to report the results of a study of the associative recall properties of the trion model. Motivated by Mountcastle's organizational principle for neocortical function (Mountcastle 1978) and by Fisher's model of physical spin systems (Fisher and Selke 1980, 1981), we (Shaw et al. 1985) developed a cooperative model of the cortical column incorporating i) an *idealized* subunit, the trion, which represents a localized group of neurons ($\sim$30–100), and ii) a discrete time step for firing ($\sim$30–100 ms). We found that networks comprised of a small number of trions (with symmetric interactions) supported up to thousands of quasi-stable, periodic firing patterns (*denoted* as MPs) which could be selected out [as in the selection principle of Edelman (1978)] using a Hebb-type algorithm for synaptic change (Hebb 1949). In the present study of the recall properties, (for a given set of network connections) by considering all possible initial firing patterns, we find 1). It takes on the average only 2–5 time steps for any initial pattern to project onto or recall an MP. 2) Many of the MPs can be individually accessed by *thousands* of different initial patterns. We present a variety of interesting examples for different couplings among the trions, illustrating the rich, general nature of the trion model. For example, we find (see Tables 1 and 2) MPs having cycle length of 18 time steps which are especially easy to recall by a huge number of initial states. We believe that these phenomena are of interest to fields of neurophysiology, cellular automata (Wolfram 1983) and molecular scale processors (Yates 1984), as possibly applied to a future generation of computers.

Despite the substantial theoretical efforts and results in modeling neural networks (see, e.g., references in MacGregor and Lewis 1977; Amari and Arbib 1982; Prisco 1984) the basis for the tremedous *magnitudes* of the processing capabilities and the memory storage capacities of mammals remain mysteries. We believe Mountcastle's (1978) columnar organizing principle for the functioning of the neocortex will provide a basis for these phenomena and we

Table 1. Properties of the MPs for the six trion network with this set of interactions from trion j to trion i. Reading left to right (see Fig. 3) are the interactions V_{ii-2}, V_{ii-1}, V_{ii}, V_{ii+1}, V_{ii+2} (and similarly for W). The number of MPs includes just the distinguishable spatial rotations. Entries in the table give only the lowest MP pattern number (see discussion associated with Eq. 2) for the set of spatially rotated MPs. The entry number of triggers denotes the percent of the 3^{12} initial patterns which project onto or trigger within 24 time steps any MP. We also give the average number of time steps for all these hits. Given here are the full firing patterns of the MPs for this network. At the top of each MP are three numbers: the number in the top row at the left simply counts the MPs, at the right is the MP pattern number and below is the number of initial patterns that trigger that MP (and its spatial rotations). Each row of an MP specifies the firing levels S_i for the six trions at a given time step (time increases from top to bottom)

Interactions
V: 1 1 1 0 0
W: 0 −1 −1 −1 0

Number of MPs: 42

Number of triggers: 82%

Avg. no. of timesteps to trigger: 3.5

1 0	2 1	3 4	4 13	5 12962	6 19448
59424	31068	13452	21804	228756	74424
− − − − − −	○ − − − − −	○ ○ − − − −	○ ○ ○ − − −	+ − − − ○ +	+ + − − − +
− − − − − −	− − − − − −	− − − − − −	− − − − − −	+ + ○ − − −	+ + + − − −
○ ○ ○ ○ ○ ○	− − ○ ○ ○ −	− − − ○ ○ −	− − − − ○ −	− + + + − −	− ○ + + ○ −
+ + + + + +	+ ○ + + + +	+ ○ ○ + + +	+ ○ ○ ○ + +	− − + + + ○	− − − + + +
+ + + + + +	+ + + + + +	+ + + + + +	+ + + + + +	+ − − ○ + +	+ − − − + +
○ ○ ○ ○ ○ ○	+ + + ○ ○ ○	+ + + + ○ ○	+ + + + + ○	+ + − − − +	+ + ○ − − ○
	− − ○ − − −	− − ○ ○ − −	− − ○ ○ ○ −	○ + + − − −	− + + + − −
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	+ + + + + +	+ + + + + +	+ + + + + +	− ○ + + + −	
	+ ○ ○ ○ + +	+ + ○ ○ + +	+ + + ○ + +	− − − + + +	

7 66430	8 67241	9 132860	10 265720
300	1464	2996	49
○ − ○ − ○ −	+ − ○ − + −	+ − + − + −	○ ○ ○ ○ ○ ○
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Table 2. Same as Table 1

Interactions
V: −1 1 −1 0 0
W: 0 1 −1 1 0
Number of triggers: 81%

Number of MPs: 39

Avg. no. of timesteps to trigger: 3.4

1 455 300	2 728 2996	3 1375 1464	4 41328 69228	5 41329 228756	6 74056 31068
+ ○ + ○ + ○	+ + + + + +	○ + + + ○ +	− − + − − +	○ − + − − +	○ ○ + − + ○
− − − − − −	− − − − − −	○ − − − − −	+ − − + − −	+ − − + − −	+ − + − ○ −
○ + ○ + ○ +		+ + + + + ○	○ + − ○ + −	− + − ○ + −	− + − + − +
○ − ○ − ○ −		− ○ − − − ○	− + + − + +	− ○ + − + +	○ ○ ○ − + −
+ + + + + +		+ ○ + + + +	+ − + + − +	+ − + + − +	+ − + − + ○
− ○ − ○ − ○		○ − − − − −	+ ○ − + ○ −	+ + − + ○ −	− + − + − +
		○ + ○ + + +	− + − − + −	− + ○ − + −	+ ○ ○ ○ + −
		− − ○ − − −	− − + − − +	− − + − − +	○ − + − + −
		+ ○ + + + +	+ − ○ + − ○	+ − − + − ○	− + − + − +
		− ○ − ○ − −	+ + − + + −	+ + − ○ + −	+ − ○ ○ ○ −
		+ + + ○ + +	− + + − + +	− + + − + +	+ ○ + − + −
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		− − − ○ − ○	+ − + + − +	+ − + + − ○	○ − + − ○ ○
		+ + + + + ○	+ + − + + −	+ + − + + −	+ − + ○ + −
		− − − − ○ −	− + ○ − + ○	− + ○ − + +	− + − + − +

7 74175 21804	8 93736 13452	9 133042 59424	10 265720 49
− + − + − +	○ − + − + ○	○ ○ ○ ○ ○ ○	○ ○ ○ ○ ○ ○
+ − + − ○ −	+ − + ○ ○ −	+ − + − + −	
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construct the trion model based on it. Following Mountcastle (1978), we consider the cortical column (roughly 500 microns in diameter) to be the basic network in the cortex which is comprised of small irreducible processing subunits (trions). These subunits are connected into columns or networks having the capability of complex spatial-temporal firing patterns. The creation and transformation of such patterns constitute the basic events of short-term memory and information processing. We strongly emphasize this *assumption*: that *higher*, complex mammalian cortical processes involve complex *spatial-temporal* network firing patterns; this is in contrast to the usual assumption that the "*coding*" only involves sets of neurons firing with high frequency. We are *not* suggesting that average firing is not important or that it is not a communication code. In fact, we presume that there are several codes in the central nervous system for communication among various regions with the sophistication of the code being related to the sophistication of the information processing involved *and* to the urgency of the information. For example, the sensing of perilous information *must* be responded to immediately and presumably would involve a simple alerting

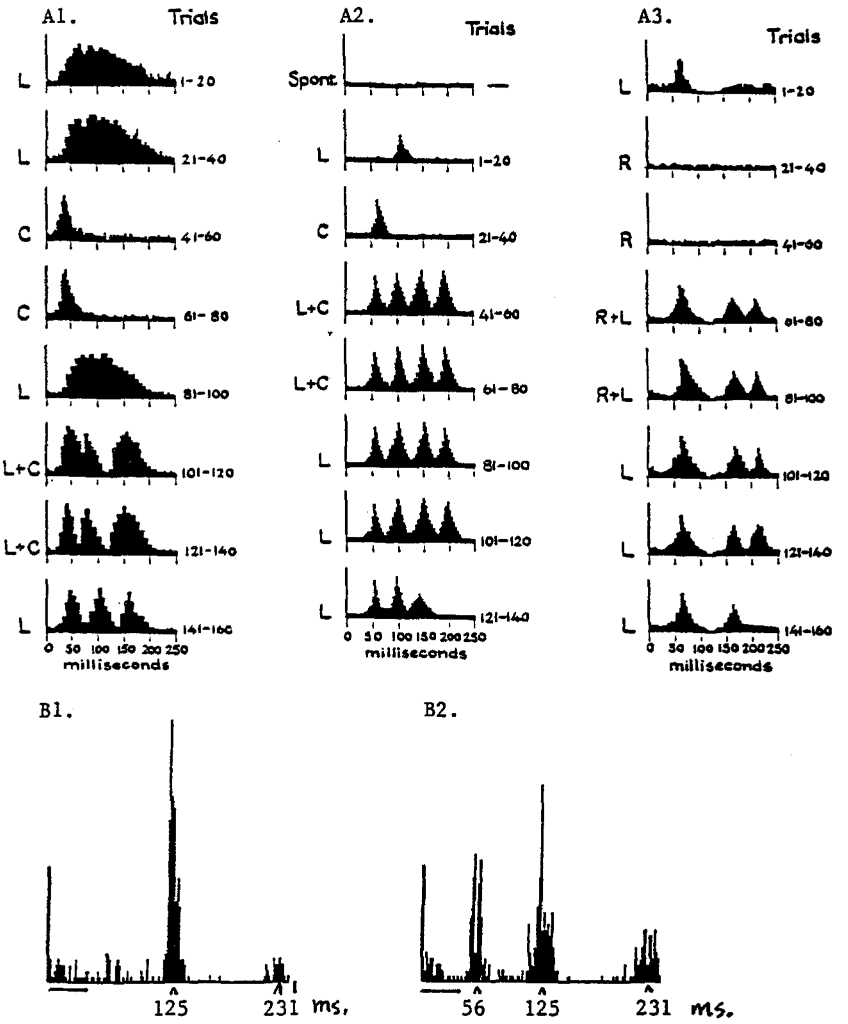

Fig. 1A and B. Single-unit data from visual area III of cat from the published work of Morrell (1967) and Morrell et al. (1983). A1, A2, and A3 are derived from Figs. 11, 14, and 12 respectively of Morrell (1967). B1 and B2 are derived from Fig. 2 of Morrell et al. (1983). **A** All stimuli were presented during the 0 to 50 ms interval. In A1 and A2 (*L*) denotes a light line, (*C*) denotes an auditory click, and (*L*+*C*) denotes simultaneous presentation of the light line and the click. In A3 the same light line was presented to the left eye (*L*), the right eye (*R*), and to both eyes (*R*+*L*). In A2 spont. denotes the spontaneous or background level of discharge. The data displayed in each histogram were acquired in consecutive sets of 20 trials, as indicated. The calibration bar at time 0 equals 20 spikes. **B** The visual stimulus was a light line presented during the time marked below the axis. The calibration bar indicates 20 spikes and about 150 trials were given. In B1 the light line was vertical while in B2 it was horizontal. These data demonstrate *possible* complex coding occuring at burst intervals of roughly 50 ms with burst levels of large, small or no peaks

code of high neuronal population firing producing a response such as the removal of a hand from a hot stove. In the opposite extreme, the composing (or recall) of a Beethoven symphony must involve incredibly precise, sophisticated spatial-temporal neuronal processes. Most processing of information probably involves several simultaneous types of coding with cortical-cortical coding and processing being more sophisticated than cortical-subcortical. We believe that the key to finding the more complex coding lies in designing multielectrode experiments (in sensory cortex) not only looking at the appropriate spatial and temporal "separations" (we suggest ~ 50–$200\,\mu$ and ~ 30–100 ms, respectively) but also presenting the appropriately simple, yet sophisticated stimuli.

We developed the trion model from the level of individual neurons to the next level or scale of phenomenological relevance which we believe to be a subunit of perhaps ~ 30–100 neurons (with only three levels of revelant firing output) and a synchronous time step ~ 30–100 ms. In making this change of scale we drew on the cortical principle of Mountcastle, our previous theoretical studies (Little and Shaw 1975, 1978; Shaw 1978; Roney and Shaw 1980) using a physical spin analogy (Ising model), the exciting work of Fisher who showed that a simple extension of the Ising model led to an *enormous* increase in richness of the solutions, our studies (Shaw et al. 1982) which suggest a subunit size of ~ 30–100 neurons, and experiments (see, e.g., Shaw et al. 1983; Morrell 1967) which show a time step of ~ 50 ms for groups of neurons bursting. [For a recent anatomical study which shows evidence for a spatial scale relevant to our trion size, see Fig. 12a of Gilbert and Wiesel (1983) which shows a clustering of axonal boutons at spacings of $90\,\mu$.]

The concept of a synchronous discrete time step $\tau \sim 50$ ms for groups of neurons to burst is crucial to our model. This should be constrasted to essentially all other models of neuronal networks (see, e.g., Hopfield 1982) in that they specifically have no "clock-like" timing. To establish the *plausibility* of such a τ, we note the observation of periodic bursting in cortex has a long history see, in particular, Morrell (1967) and Morrell et al. (1983) who found multipeak responses in cat visual cortex with peak separation of approximately 50 ms. In addition, Morrell (1967; Morrell et al. 1983) observed dramatic changes in these bursting patterns when he paired stimuli in conditioning experiments. Some of these data are shown in Fig. 1. We suggest that these burst pattern data might be *consistent* with exciting or enhancing different periodic firing patterns (MPs) in our trion model. In addition to the simulation studies reported in this paper, we have conducted neurophysiological experiments (Shaw et al. 1983; Pearson 1985) to test certain assumptions of the model. We presented in Fig. 2 of Shaw et al. (1985) some of our data from cat primary visual cortex recording from a group of 2–3 neurons which show *four equally* spaced peaks in the post-stimulus histogram in response to a flashed bar [also see Fig. 1 of (Shaw et al. 1983)]. These peaks are separated by approximately 50 ms in close agreement with Morrell's data in Fig. 1. Also, as a result of showing time sequences of different bar orientations we observed burst patterns which might be consistent with exciting MPs. An excellent example of these data is given in Fig. 2. Clearly, it would be very interesting to record simultaneously from two or more closely spaced microelectrodes to test our assumption of a discrete time step τ.

The following features of the trion model are all necessary for its qualitative richness:

a) Finite fluctuations due to the random nature of synaptic transmission as well as other sources of noise.

b) Three possible firing states S (of each trion) denoted by $+(+1), 0, -(-1)$ which represent, respectively, a large "burst" of firing, an average burst, and a below average firing.

c) Associated with each of the three trion states S is a statistical weighting term $g(S)$ with $g(0) \gg g(+)$, $g(-)$ which takes into account the number of equivalent firing configurations of the trion's internal neuronal constituents. (For example, in a group of 90 neurons, firing levels of $+, 0$, and $-$ could correspond to $90-61$, $60-31$, $30-0$ neurons firing. There are many more combinatorial ways of generating the $60-31$ level.) This crucial feature $g(0) \gg g(+)$, $g(-)$ gives the firing patterns stability.

d) Synchronous discrete time steps τ ($\gg$ the firing time $\sim$ms of the individual neurons). We update the state of the system at time $n\tau$ in a probabilistic way related to the states at the *two* previous time steps $(n-1)\tau$ and $(n-2)\tau$.

e) A highly symmetrical interplay of inhibition and excitation among the interactions connecting the trions.

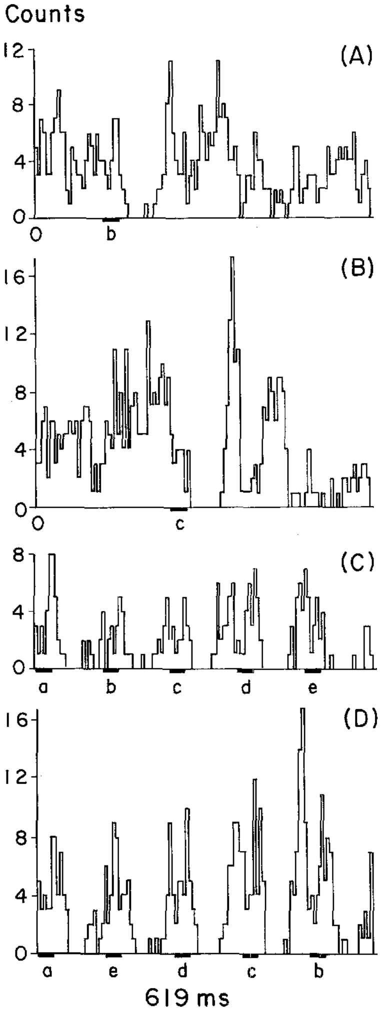

Fig. 2A–D. Spike firing responses of a cluster of three neurons in area 17 of a cat to four different time sequences of an oriented, flashed bar [see Shaw et al. (1983) and Pearson (1985) for more details]. There were 30 (continuous) cycles of 619 ms duration for each poststimulus histogram. The on times for the flashed bar on each cycle are denoted by the bars (33 ms duration) on the time axis and the subscripts *a, b, c, d, e* represent orientation angles of 0°, 36°, 72°, 108°, 144° respectively. We point out two major experimental results indicated by these data, revelant to our trion model. i) In response to each bar, there are two peaks, separated by ~100 ms in the presentations **A** and **B** of a single bar per cycle and by ~50 ms in the clockwise **C** and counter clockwise **D** series of 5 bars. ii) The response in the counterclockwise sequence **D** is substantially greater than that for the clockwise sequence **C**. We believe that both these striking effects i) and ii) for these preliminary data are consistent with exciting MPs in our trion model with a time step $\tau \sim 50$ ms

The probability $P_i(S)$ of the i^{th} trion attaining state S at time $n\tau$, is given by:

$$P_i(S) = \frac{g(S) \cdot \exp[B \cdot M_i \cdot S]}{\sum_s g(s) \cdot \exp[B \cdot M_i \cdot s]}, \tag{1}$$

$$M_i = \sum_i [V_{ij} \cdot S'_j + W_{ij} \cdot S''_j] - V_i^T,$$

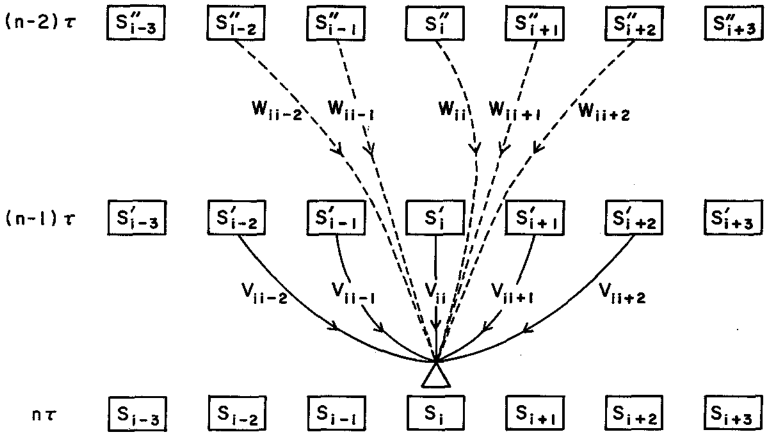

Fig. 3. Shown schematically is a network of N trions at three time steps. Each trion i has connections (*solid lines*) in one time step $(n-1)\tau$ to $n\tau$ from itself with strength V_{ii}, its nearest neighbors with strength $V_{ii\pm 1}$ and its next-nearest neighbors $V_{ii\pm 2}$. There are similar connections (*dotted lines*) W_{ij} in two time steps, $(n-2)\tau$ to $n\tau$. The probability for the firing level S_i of trion i is determined by the shown connection strengths, and the firing levels S'_j and S''_j (of the connected trions) at times $(n-1)\tau$ and $(n-2)\tau$ through (1). There are cyclic or ring-like boundary conditions so that trion i = trion $i+N$

where S'_j and S''_j are the states of the j^{th} trion at times $(n-1)\tau$ and $(n-2)\tau$ respectively. V_{ij} and W_{ij} are the interactions between trions i and j between time $n\tau$ and times $(n-1)\tau$ and $(n-2)\tau$ respectively. V_i^T is an effective firing threshold. [Following (Little and Shaw 1978; Roney and Shaw 1980), $V_i^T = [2V_i - \sum (V_{ij} + W_{ij})]$ with V_i the threshold for the firing of the i^{th} trion.] B is inversely proportional to the level of noise, "temperature", or random fluctuations in the system. The deterministic limit is taken by letting B approach infinity, (analogous to the noise approching zero), in which case the $S=0$ states vanish. (See the discussion below associated with Fig. 4.)

Equation (1) completely determines our trion model. All the networks that we consider in this paper have $g(+)=1$, $g(0)=500$, $g(-)=1$, $V_i^T=0$, six trions, and cyclic boundary conditions (i.e., the trions connected in a ring). The V_{ij} and W_{ij} are considered out to (including) next nearest neighbours as illustrated in Fig. 3. For a given set of parameters, V_{ij}, W_{ij}, $g(S)$, and B, we examine *all* $3^{6+6} = 531{,}441$ possible firing configurations of the first two time steps. The computer is

Table 3. Same as Table 1. We note that only interactions lasting one time step are present. Thus there are really only 3^6 initial patterns. However, to keep a format similar to the other tables, we consider all 3^{12} time step patterns

Interactions — Number of MPs: 172

V: −1 0 2 0 −1

W: 0 0 0 0 0

Number of triggers: all — Avg. no. of timesteps to trigger: 1.8

1 5840 39366 ++−−−−	2 12410 13122 ++o−−−	3 18250 13122 o++−−−	4 18980 39366 +++−−−	5 25550 13122 ++−o−−	6 32120 4374 ++oo−−
7 37960 4374 o++o−−	8 38690 13122 +++o−−	9 40880 19683 +−−+−−	10 43070 13122 +o−+−−	11 45260 39366 ++−+−−	12 47450 13122 +−o+−−
13 49640 4374 +oo+−−	14 51830 13122 ++o+−−	15 53290 13122 o−++−−	16 54020 39366 +−++−−	17 55480 4374 oo++−−	18 56210 13122 +o++−−
19 57670 13122 o+++−−	20 58400 39366 ++++−−	21 70810 39366 o+o−o−	22 84680 4374 ++−oo−	23 90520 13122 o+ooo−	24 102200 2187 +o−+o−
25 104390 13122 ++−+o−	26 108040 13122 ooo+o−	27 110230 39366 o+o+o−	28 143080 2187 o+−o+−	29 143810 13122 ++−o+−	30 163520 19683 ++−++−
31 265720 6561 oooooo					

then instructed to search for all the quasi-stable, periodic firing patterns (MPs) which have a high probability of cycling. The MPs are found by computing the most probable temporal evolution of the trion states from each of the possible initial conditions using (1) and determining if that evolution leads to a pattern that repeats after some time steps with a high probability (an MP). Thus this calculation for a given network (set of parameters) yields all the MPs as well as how many of the 531,441 initial conditions lead to each MP and how many time steps it takes. We have computed more than 40 examples of such six trion networks, each of which takes several hours of VAX 780 time.

Listed in Tables 1–6 are 6 examples of six trion networks [all with $g(\pm)=1$, $g(0)=500$, and $V_i^T=0$]. All MPs having a probability of cycling $>10\%$ for (fluctuation parameter) $B=10$ are given in each table. The MP pattern number is a two time step firing configuration number as a 12 digit ternary number (with $-=0$, $0=1$ and $+=2$) converted to a base 10 number and (along with the interaction strengths) completely defines the pattern. Thus the first MP in Table 1 has pattern number 0 which is $\begin{matrix} - & - & - & - & - & - \\ - & - & - & - & - & - \end{matrix}$ as the starting configuration. The given interactions are readily used in (1) to calculate the full 6 cycle MP as

$$\begin{matrix} - & - & - & - & - & - \\ - & - & - & - & - & - \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ + & + & + & + & + & + \\ + & + & + & + & + & + \end{matrix} \tag{2}$$

In Table 1, the second MP has pattern number 1 corresponding to $\begin{matrix} 0 & - & - & - & - \\ - & - & - & - & - \end{matrix}$ and the time evolution leads to an 18 cycle pattern. For this 18 cycle MP there are 18 *equivalent* starting positions (or time rotations), only the lowest pattern number is listed. In addition, this MP has 6 *inequivalent* spatial rotations; we regard each individual trion as distinguishable. Thus we consider this MP to have 5 *additional distinguishable* spatial rotations; however only the lowest pattern number is listed. [Note that MP pattern number 0, (2), has *no distinguishable* spatial rotations.] We list the number of starting conditions which lead to that MP (along with all the MP's time and spatial rotations). Since the major computing effort is to find the MPs for a given network, these tables represent a *valuable* data base for readily performing *many* other calculations in the trion model, e.g., reinforcing individual MPs using the Hebb algorithm (3). [Substantial changes ($\lesssim 20\%$) in the interactions away from the "symmetric" values listed in the tables introduce no new MPs.] As another example, Fig. 4 gives the probabilities of cycling for two of the MPs in Table 6 as a function of the fluctuations parameter B for the symmetric interaction case and a somewhat asymmetric case. (This figure was *readily* calculated using the MP pattern numbers from Table 6.) Figure 4 illustrates an important feature of the trion model: Both for small fluctuations (large B) and large fluctuations [small B, where roughly we compare $\exp(BM_i)$ in (1) to $g(S)$], the probabilities of cycling go to zero (for asymmetry in the interactions) for any MP having $S=0$ (together with $S=\pm 1$) levels. Thus finite fluctuations are *crucial* for the full richness of the model.

Now we discuss the striking results of our calculations:

1) Rapid Nature of the Recall Process. The average number of time steps that it takes a starting configuration to trigger an MP ranges from $\sim$2–5. Each of the 3^{12} starting configurations is followed (for a given network) for up to 24 time steps until it triggers or excites an MP, and an average number of time steps is

Table 4. Same as Table 1

Interactions | Number of MPs: 216

V: 0 −1 1 −1 0

W: 0 1 −1 1 0

Number of triggers: all | Avg. no. of timesteps to trigger: 4.1

1 215	2 239	3 455	4 728	5 944	6 968
288	288	300	7988	132	384
+++o+−	+o+++−	+o+o+o	++++++	+++o+−	+o+++−
−−−−−−	−−−−−−	−−−−−−	−−−−−−	o−−−−−	o−−−−−
o+++−+	−+++o+	o+o+o+		++++−+	o+++o+
−−−o−+	−o−−−+	−o−o−o		−−−o−+	−o−−−+
++++++	++++++	++++++		o+++++	o+++++
o−−−+−	+−−−o−	o−o−o−		−−−−+−	o−−−o−

Table4 (continued)

7 1184	8 1208	9 1295	10 1367	11 1375	12 1424
516	384	96	516	660	132
+ o + o + o	+ − + + + o	+ + + + − +	+ + o + o +	o + + + o +	+ − + o + +
o − − − − −	o − − − − −	o − − − − −	o − − − − −	o − − − − −	o − − − − −
+ + o + o +	o + o + + +	+ + + o + −	+ o + o + o	+ o + + + −	+ + − + + +
− o − o − o	− + − − − o	− − − − + −	− − o − o −	o − − − o −	− + − o − −
o + + + + +	o + + + + +	o + + + + +	o + + + + +	o + + + + +	o + + + + +
− − o − o −	o − o − − −	− − − o − +	− o − o − o	− o − − − +	− − + − − −
13 1439	14 1447	15 1700	16 2102	17 7748	18 20888
96	660	132	132	2568	498
+ + − + + +	o + o + + +	+ + + + + −	+ o + + o +	+ + + o + o	+ + o + + o
o − − − − −	o − − − − −	+ − − − − −	+ − − − − −	o − o − − −	o − − o − −
+ − + o + +	+ − + + + o	+ o + + o +	+ + + + + −	+ o + + o +	+ o + + o +
− − + − − −	o − o − − −	− − − − − +	− o − − o −	− − − o − o	− − o − − o
o + + + + +	o + + + + +	− + + + + +	− + + + + +	o + o + + +	o + + o + +
− + − o − −	− + − − − o	− o − − o −	− − − − − +	− o − − o −	− o − − o −
19 21056	20 27908	21 28262	22 40880	23 41033	24 41048
498	7968	7968	1422	67824	23736
+ o + + o +	+ + o o + −	+ − + + − +	+ − − + − −	+ − + o + −	+ + − + + −
o − − o − −	+ − o o − −	+ − o o − −	+ − − + − −	+ − − + − −	+ − − + − −
+ + o + + o	+ − + + − +	+ + o o + −	o o o o o o	o + − + − +	+ − + + − +
− o − − o −	− − o o − +	− + − − + −	− + + − + +	− + − o − +	− − + − − +
o + + o + +	− + o o + +	− + o o + +	− + + − + +	− + + − + +	− + + − + +
− − o − − o	− + − − + −	− − o o − +	o o o o o o	o − + − + −	− + − − + −
25 41216	26 41384	27 43070	28 43232	29 43564	30 45260
5250	23736	1248	3852	3852	912
+ o o + o o	+ − + + − +	+ o − + − −	+ o − + + −	o o o + − +	+ + − + − −
+ − − + − −	+ − − + − −	+ o − + − −	+ o − + − −	+ o − + − −	+ + − + − −
+ o o + o o	+ + − + + −	o o o o o o	o o o + − +	+ o − + + −	o o o o o o
− o o − o o	− + − − + −	− o + − + +	− o + − − +	o o o − + −	− − + − + +
− + + − + +	− + + − + +	− o + − + +	− o + − + +	− o + − + +	− − + − + +
− o o − o o	− − + − − +	o o o o o o	o o o − + −	− o + − − +	o o o o o o
31 45394	32 45506	33 47450	34 73811	35 74182	36 82040
672	672	1248	93504	110088	270
o + − o + −	+ − o + − o	+ − o + − −	+ − + − + −	o o o + − +	+ o o + o o
+ + − + − −	+ + − + − −	+ − o + − −	+ − + − o −	+ − + − o −	o o − o o −
+ − − + − +	− + − + + −	o o o o o o	o o o + − +	+ − + − + −	o + o o + o
o − + o − +	− + o − + o	− + o − + +	− + − + − +	o o o − + −	− o o − o o
− − + − + +	− − + − + +	− + o − + +	− + − + o +	− + − + o +	o o + o o +
− + + − + −	+ − + − − +	o o o o o o	o o o − + −	− + − + − +	o − o o − o
37 82096	38 93494	39 102200	40 102256	41 102368	42 103660
270	71724	2340	510	510	1728
o + o o + o	+ − + − + −	+ o − + o −	o + − o + −	+ − o + − o	o + − + o −
o o − o o −	+ − + o o −	+ o − + o −	+ o − + o −	+ o − + o −	o + − + o −
+ o o + o o	o o − + − +	o o o o o o	+ − o + − o	o + − o + −	o o o o o o
o − o o − o	− + − + − +	− o + − o +	o − + o − +	− + o − + o	o − + − o +
o o + o o +	− + − o o +	− o + − o +	− o + − o +	− o + − o +	o − + − o +
− o o − o o	o o + − + −	o o o o o o	− + o − + o	o − + o − +	o o o o o o
43 132860	44 265720				
83820	49				
+ − + − + −	o o o o o o				
+ − + − + −					
o o o o o o					
− + − + − +					
− + − + − +					
o o o o o o					

Table 5. Same as Table 1

Interactions
V: 0 −1 1 1 0
W: −1 0 −1 0 1
Number of triggers: 100%

Number of MPs: 85
Avg. no. of timesteps to trigger: 3.8

1 0 54	2 91 44	3 5856 114198	4 12444 20958	5 18300 12312	6 19032 105954
− − − − − −	o − o − o −	− + + − − −	− + + o − −	− o + + − −	− + + + − −
− − − − − −	− − − − − −	+ + − − − −	+ + o − − −	o + + − − −	+ + + − − −
o o o o o o	− o − o − o	+ − − − − +	+ o − − − +	+ + − − − o	+ + − − − +
+ + + + + +	o + o + o +	− − − − + +	o − − − + +	+ − − − o +	+ − − − + +
+ + + + + +	+ + + + + +	− − − + + −	− − − + + o	− − − o + +	− − − + + +
o o o o o o	+ o + o + o	− − + + − −	− − + + o −	− − o + + −	− − + + + −

7 38064 2232	8 38796 12312	9 40992 19914	10 40993 34056	11 43206 32376	12 51972 20844
− o + + o −	− + + + o −	− + − − + −	o + − − + −	− + − o + −	− + + o + −
o + + o − −	+ + + o − −	+ − − + − −	+ − − + − −	+ o − + − −	+ + o + − −
+ + o − − o	+ + o − − +	o − + o − +	− − + o − +	+ − + − − +	+ o + − − +
+ o − − o +	+ o − − + +	− + + − + +	− + + − + o	− + o − + +	o + − − + +
o − − o + +	o − − + + +	+ + − + + −	+ + − + + −	o + − + + −	+ − − + + o
− − o + + o	− − + + + o	+ − o + − o	+ − o + − +	+ − + + − −	− − + + o +
		− − + − − +	− − + − o +	− o + − − +	
		− + − − + −	− + − − + −	− + − − + o	
		+ o − + o −	+ o − + − −	+ − − + + −	
		+ − + + − +	+ − + o − +	o − + + − +	
		− + + − + +	− + + − + +	− + + − o +	
		o + − o + −	o + − + + −	+ + − − + −	
		+ − − + − −	+ − o + − −	+ − − + − o	
		− − + − − +	− − + − − +	− − + o − +	
		− + o − + o	− + − − + o	− + + − + −	
		+ + − + + −	+ o − + + −	+ + − + o −	
		+ − + + − +	+ − + + − +	+ − o + − +	
		− o + − o +	− + + − o +	− − + − + +	

13 53436 20844	14 57828 20958	15 58560 114198	16 66430 28	17 66521 44	18 132860 54
− o − + + −	− o + + + −	− + + + + −	o − o − o −	+ − + − + −	+ − + − + −
o − + + − −	o + + + − −	+ + + + − −	o − o − o −	o − o − o −	+ − + − + −
− + + − − o	+ + + − − o	+ + + − − +	o o o o o o	− o − o − o	o o o o o o
+ + − − o −	+ + − − o +	+ + − − + +	o + o + o +	− + − + − +	− + − + − +
+ − − o − +	+ − − o + +	+ − − + + +	o + o + o +	o + o + o +	− + − + − +
− − o − + +	− − o + + +	− − + + + +	o o o o o o	+ o + o + o	o o o o o o

19 265720 1
o o o o o o

computed from that (large) percentage of the 3^{12} that trigger in the 24 time steps.

2) MPs *Recalled by Many Initial Patterns.* We note that large numbers of individual MPs are accessed or triggered by many *thousands* of initial configurations.

3) *Long Time Cycle* MPs *Triggered by Huge Number of Initial States.* MPs with cycle lengths of 18τ are given in Tables 1, 2, and 5. Especially interesting are MPs 12962 in Table 1 and 41329 in Table 2 each of which is accessed by almost half of the 3^{12} initial patterns!

4) *Rich, general nature of the trion model.* These examples of networks with different connections among the trions illustrate the great variety of different behaviour possible in the model: We examined six trion networks that supported *very large* numbers of MPs. For example the network having interactions V: 0 1 0 1 0 and W: −1 0 0 0 −1 (see Table 1 for notation) had 1804 MPs; the network with V:

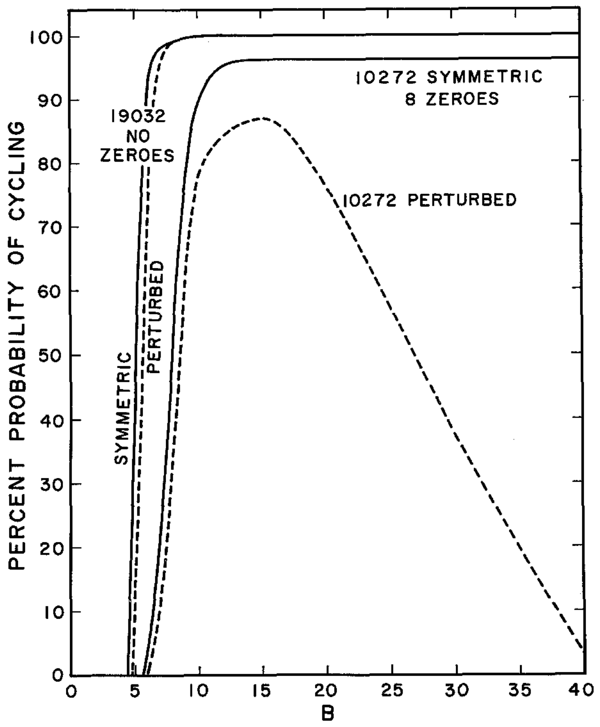

Fig. 4. Plot of probability P of cycling versus fluctuation parameter B for two MPs from Table 6. The solid curves correspond to the symmetric Vs and Ws given in Table 6; the dotted curves correspond to the perturbed values of the interactions given by

V: 0 1.05 1.00 0.94 0

W: 0 −0.95 −0.98 −1.02 0.

These curves are calculated using (1). Small B corresponds to large fluctuations, and large B to small fluctuations. We see that the probability P for MP 10272 (with 8 zero firing states) goes to zero both at large *and* small B for the *perturbed* interactions whereas P for MP 19032 (with no zero firing states) remains large in the deterministic limit. This demonstrates that fluctuations are crucial to obtain large probabilities of cycling for most of the MPs in our model

0 1 1 1 0 and W: −1 −1 1 −1 −1 had 861 MPs. Then we note the many simple 1 cycle MPs in Table 3 as contrasted to the complex 18 cycle MPs in Tables 1, 2, and 5. Perhaps networks of the type given in Table 3 with only limited temporal patterning might be more relevant for primary sensory areas of cortex whereas the quite complex 18 cycle patterns might be relevant in the higher association area. Along this latter point see the discussion below on the association or sequencing between MPs.

We have seen that the initial patterns which are just parts of the full MP cycle can be a *very small* percentage of the patterns which excite the MP. Thus we have a very general "associative" recall capability of the network. The rapid projection of initial patterns onto individual MPs, as demonstrated in Tables 1–6, is one level or mode by which the Trion model supports associative recall. This mode essentially specifies the mapping between the external signals which set the initial states and the MPs which represent them. We have also investigated another "higher" level or mode of associative recall, whereby one MP can recall another (Pearson 1985).

The sequence of states making up a MP is the most probable sequence, and, as shown in Fig. 4, they have a high probability of repeating. However, due to the stochastic nature of (1), there is a small but finite probability that an "error" will occur at some point in the propagation of a MP. This "error" then initiates a new sequence of states which leads to the triggering of another MP. There are many (3^6-1) possible errors at each time step, and if external signals are involved any one of them is likely. However, if one considers errors caused by chance, then by far the most likely errors are those in which only one of the six trions is different from its MP value. It is this class of single trion errors which we have studied. There are three key features of such noise induced transitions between MPs: 1) The number of time steps between the exit from the initial

Table 6. Same as Table 1

Interactions
V: 0 1 1 1 0
W: 0 −1 −1 −1 0

Number of MPs: 246

Number of triggers: all

Avg. no. of timesteps to trigger: 4.1

1 0	2 1	3 4	4 13	5 756	6 5840
83820	110088	71724	93504	67824	912
− − − − − −	o − − − − −	o o − − − −	o o o − − −	− − − o − −	+ + − − − −
− − − − − −	− − − − − −	− − − − − −	− − − − − −	o − − − − −	+ + − − − −
o o o o o o	− − o o o −	− − − o o −	− − − − o −	+ + − − − +	o o o o o o
+ + + + + +	o + + + + +	o o + + + +	o o o + + +	+ + + o + +	− − + + + +
+ + + + + +	+ + + + + +	+ + + + + +	+ + + + + +	o + + + + +	− − + + + +
o o o o o o	+ + o o o +	+ + + o o +	+ + + + o +	− − + + + −	o o o o o o

Table 6 (continued)

7 5856 672 −++−−− ++−−−− +o−−o+ +−−+++ −−++++ −o++o−	8 6320 672 +−−−−+ ++−−−− o++o−− −++++− −−++++ o−−o++	9 8268 288 −+−−−o +−o−−− −+−+−+ +−+++o −+o+++ +−+−+−	10 8295 384 −+−o−o +−o−−− −+−o−+ +−+o+o −+o+++ +−+o+−	11 8322 96 −+−+−o +−o−−− −+−−−+ +−+−+o −+o+++ +−+++−	12 8511 132 −+−−−+ +−o−−− −+−+−o +−+++− −+o+++ +−+−+o
13 8538 660 −+−o−+ +−o−−− −+−o−o +−+o+− −+o+++ +−+o+o	14 8565 288 −+−+−+ +−o−−− −+−−−o +−+−+− −+o+++ +−+++o	15 9552 3852 −o++−− ooo−−− +o−−−+ +o−−++ ooo+++ −o+++−	16 9968 3852 +o−−−+ ooo−−− −o++−− −o+++− ooo+++ +o−−++	17 10272 7968 −oo+−− +oo−−− ++−−−+ +oo−++ −oo+++ −−+++−	18 10700 7968 ++−−−+ +oo−−− −oo+−− −−+++− −oo+++ +oo−++
19 11680 1728 o+o−−− o+o−−− oooooo o−o+++ o−o+++ oooooo	20 12410 1248 ++o−−− ++o−−− oooooo −−o+++ −−o+++ oooooo	21 13911 132 −+−+−− o−+−−− −+−o−+ +−+−++ o+−+++ +−+o+−	22 14127 384 −+−o−o o−+−−− −+−+−o +−+o+o o+−+++ +−+−+o	23 14154 660 −+−+−o o−+−−− −+−o−o +−+−+o o+−+++ +−+o+o	24 14370 96 −+−o−+ o−+−−− −+−+−− +−+o+− o+−+++ +−+−++
25 14640 132 −+−+−− +−+−−− o+−o−+ +−+−++ −+−+++ o−+o+−	26 15072 132 −+−−−+ +−+−−− −+o+−o +−+++− −+−+++ +−o−+o	27 18250 1248 o++−−− o++−−− oooooo o−−+++ o−−+++ oooooo	28 18980 1422 +++−−− +++−−− oooooo −−−+++ −−−+++ oooooo	29 19032 23736 −+++−− +++−−− ++−−−+ +−−−++ −−−+++ −−+++−	30 19240 5250 o+oo−o +++−−− o+oo−o o−oo+o −−−+++ o−oo+o
31 19448 23736 ++−−−+ +++−−− −+++−− −−+++− −−−+++ +−−−++	32 37960 2340 o++o−− o++o−− oooooo o−−o++ o−−o++ oooooo	33 38064 510 −o++o− o++o−− ++o−−o +o−−o+ o−−o++ −−o++o	34 38168 510 ++o−−o o++o−− −o++o− −−o++o o−−o++ +o−−o+	35 66612 300 −o−o−o o−o−o− −+−+−+ +o+o+o o+o+o+ +−+−+−	36 66615 516 −+−o−o o−o−o− −o−+−+ +−+o+o o+o+o+ +o+−+−
37 66642 516 −+−+−o o−o−o− −o−o−+ +−+−+o o+o+o+ +o+o+−	38 67368 2568 −o−+−o +−o−o− o+−o−+ +o+−+o −+o+o+ o−+o+−	39 76128 498 −+o+−o +o+−o− o+−o−+ +−o−+o −o−+o+ o−+o+−	40 76336 498 o+−o−+ +o+−o− −+o+−o o−+o+− −o−+o+ +−o−+o	41 95056 270 o+oo−o oo+oo− −oo+oo o−oo+o oo−oo+ +oo−oo	42 95160 270 −oo+oo oo+oo− o+oo−o +oo−oo oo−oo+ o−oo+o
43 133224 7988 −+−+−+ +−+−+−	44 265720 49 oooooo				

MP (due to the error) to the triggering of the final MP is small (e.g. average 1–5). Thus, as with the input mapping type of recall shown in Tables 1–6, recall is rapid. 2) The probability of the most probable sequence of states between MPs is very high. Thus, once an error is made in an initial MP, the identity of the final MP is almost certain – i.e., such transitions are reliable. 3) The MPs are organized into classes. Each class is defined by the MPs which it can trigger, and by the MPs which can trigger it. Thus, even though these transitions are triggered by chance events, they form an ordered "sequence" when viewed as a whole. As an example of these sequences of spontaneous transitions among MPs, see Fig. 1 of Shaw et al. (1985) which shows a Monte Carlo simulation (of the network in Table 1) with 6 rapid transitions.

Previously, we had shown (Shaw et al. 1985) that introducing an idealized substructure, the trion, in modeling the cortical column led to a selective, adaptive network. Networks composed of a small number of trions (with symmetric interactions) supported up to thousands of MPs, any of which could be selected out with only small changes in interaction strengths using the Hebb-type algorithm

$$\begin{aligned} \Delta V_{ij} &= \varepsilon \sum_{\text{cycle}} S_i(\tau) S_j(\tau-1) \\ \Delta W_{ij} &= \varepsilon \sum_{\text{cycle}} S_i(\tau) S_j(\tau-2), \qquad \varepsilon > 0 . \end{aligned} \tag{3}$$

We note that the 18 cycle MPs in Tables 1, 2, and 5 found in the present study were also able to be enhanced using (3). We speculate that these symmetrical interactions might be specified genetically giving a "naive" network which could initially respond to many different input signals. Experience or learning could then modify the connections via a Hebb type mechanism (3) to select out (as in the work of Edelman 1978) the appropriate responses or MPs.

The striking results presented here on the associative recall properties of the trion model give further encouragement to continued theoretical studies on this rich, general model which we believe embodies a basis for a theory of information processing and memory. However, the success of this (or any model) rests on possible experimental verification. Experiments which present dynamical sequences of stimuli to awake animals and record spikes from multiple microelectrodes in (somatosensory) cortex will be performed in the laboratory of M. Merzenich. We believe that the results of these experiments (looking for spatial-temporal neuronal firing patterns) will indeed test the trion model. We conclude by stressing the importance in our model (of the cortical column, ~500–100 μ diameter) of having both a spatial subunit scale (~50–200 μ) and a clock-like temporal scale (~30–100 ms) present. Clearly there is no conclusive evidence for these scales, however, more and more supportive data are being found in the central nervous system of mammals in both anatonical and physiological experiments (Gilbert and Wiesel 1983; Morrell 1967; Morrell et al. 1983; Mountcastle 1978; Pearson 1985; Shaw et al. 1982, 1983).

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