

Attractor neural networks and biological reality: associative memory and learning

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It is argued, in the light of recent neurophysiological findings, that neural networks (cell assemblies) whose connectivity involves strong feedback and which consequently can sustain patterns of high spiking activity (reverberations), are plausible descriptions of cognitive function in certain cortical regions. Such networks can store a high number of different memories and perform associative retrieval effectively, even in the presence of high levels of noise, synaptic damage and neuronal sloppiness. Such Attractor Neural Network (ANNs) produce emergent signals which indicate the completion of a computation. Moreover, the existence of the attractors provides a candidate for memory on the shortest scale, which does not call for synaptic changes; as such the attractors are natural candidates for Hebbian learning.

Recent extensive data analysis of recordings from performing monkeys puts rather severe upper bounds on the spike rates in some regions of cortex, in which enhanced rates are observed. These findings favor a class of models of ANNs which have stochastic attractors whose spike rates are tunable by the level of the overall inhibition. While these models include significant modifications of the original ANNs, they belong conceptually to the same class, in terms of computation, effectiveness and robustness.

Finally, we remark on a possible reinterpretation of recent empirical biochemical findings that can provide a realistic mechanism for Hebbian learning.

1. Empirical evidence for reverberation attractors

Neurophysiology is always attracted to brain regions in which neuronal spiking activity is enhanced in correlation with computational (cognitive) performance. Such enhanced spiking rates may be the result of afferent potentials. Or, alternatively, they may be due to the network's reverberations sustained by a strong feedback mechanism. The existence of strong synaptic feedback, as well as the selectivity to particular distribution of enhanced activity among the neurons of the network (patterns), are determined by the special matrix of synaptic strengths (see e.g. [1,2,3]). In that case the role of the afferents is restricted to the provocation of a particular pattern of reverberation (an attractor) [4]. An entire class of such afferents (stimuli) brings about the same reverberation, i.e. leads to the same attractor which is represented by the subset of neurons whose spiking rates are enhanced by the particular stimulus. In this second scenario, the arrival from a stimulus to the attractor is the articulation of an elementary *associative recall* from memory.

I suggest that the structured synaptic feedback is a rather likely account for the cognitively enhanced neuronal spiking activity, at least in some cortical regions in which significant cognitive functioning takes place. Setting aside introspective evidence, one can find positive support in the remarkable experiments of Miyashita and Chang [5], in which the enhanced activity, correlated with abstract feature recognition, is sustained for 16 seconds following the removal of the stimulus. Fig. 1 reproduces the results of [5] on short term memory. It exhibits the number of spikes per second, emitted by a given neuron in the anterior ventral temporal cortex of a monkey (*macaca fuscata*), as a function of time. The graphs in the figure represent the results of an entire experimental procedure. Under the graph is a presentation of the stimuli schedule: first there is a warning light (0.5 sec); followed immediately by a visual pattern (0.2 sec); the pattern is removed for 16 seconds; then a matching pattern is presented (0.2

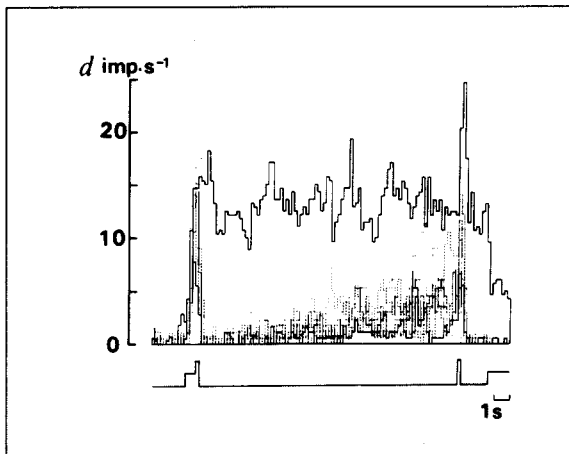


Fig. 1. Graphs of spiking rates of one neuron in the anterior ventral temporal cortex of a monkey. Top curves are rates upon presentation of four transformed versions of the same visual stimulus. Low curves are the reactions of the same neuron to different stimuli. At bottom of each graph is the stimulus schedule, see text. From [5].

sec). The last stimulus on the far right of each schedule is a choice signal, to allow the monkey to react selectively if he considers the matching pattern the same as initial one or different from it.

The experiments compare the reactions in the same neuron upon presentation of four pattern stimuli, which are transformed versions of each other, in scale, orientation and color. The high curve in the graph is the activity of that neuron upon presentation of one of four transformed versions of a pattern to which that neuron is most sensitive. The low curves are the activities of the same neuron upon presentation of different patterns, to which it is known to be insensitive. The neuron is selected to be one which is sensitive to a single pattern, out of a couple of a hundred neurons that were measured, and which typically were sensitive to more than one pattern. Miyashita and Chang [5] focus on the impressive fact of the existence of neurons which *detect* and *remember* an *abstract* feature, namely the underlying shape:

- Detection – is the elevated spike rate of the neuron.
- Remembrance – is the persistence of the elevated spike rate for 16 seconds.
- Abstractness – is the similarity of the four reactions to the four transformed stimuli.

These are very impressive findings indeed. But they attain an additional dimension in the present context upon a change of emphasis:

- A stimulus leading to a neural reaction unambiguously raises the spiking rates of a group of neurons. In the data the increase is from 1–2/s to 10–15/s.
- The enhanced spiking rates persist for 16 seconds, after the stimulus has been removed.
- More than one neuron reacts to a certain stimulus and some of the neurons react to multiple stimuli.

The fact that a given neuron can sustain its raised spiking rate for 16 seconds, which is a couple of thousand times any conceivable neuronal time scale is pregnant with implications. It necessarily implies that:

- It is not the stimulus which sustains the enhanced spiking rates.
- The neuron cannot go it alone, it must be a member of an assembly of neurons – a neural network.
- The enhanced spiking activity is an extremely stable reverberation mode of the network – an attractor.
- An attractor is characterized by the specific collection of neurons whose rates are enhanced by a given stimulus.

One can also find negative support for the independence from stimulus of computationally enhanced rates in the experiments of Anderson and Mountcastle [6], in which the enhanced activity, correlated with the stimulus, decays while the stimulus is still present. Finally, it is amusing to note that the removal of the system from the very stable attractor, by the matching stimulus on the right end of the stimulus schedule, is very reminiscent of the behavior of a network of short term memory, designed to count chimes [7].

2. Models of ANNs and the low rate problem

Some of the elements and results of the modeling effort of ANNs, that has been instigated by Hopfield [3], have been reviewed in a tutorial at this meeting. A detailed description of this approach can be found in [8] and in references therein. Here I will restrict myself to a brief recapitulation of results relevant to the present discussion.

2.1 Description of the network

The network consists of N 'neurons' each of which can have a synaptic connection to any other. The synaptic efficacy connecting the axon of neuron j to the soma (via a dendrite) of neuron i is denoted by J_{ij} . At discrete time intervals every neuron considers, asynchronously, the post synaptic potential (PSP) arriving at its soma. The PSP is a linear sum of the synaptic efficacies afferent on this neuron from all other neurons which have emitted a spike in the previous time interval. The neuron then compares the resulting depolarization to its threshold and the net depolarization determines the probability that the neuron will emit a new spike.

Before formalizing somewhat this description, a few clarifying comments:

- The network is not intended as a description of the entire cortex, or as a major part of it. Rather, it is viewed as a small module, consisting of 1000–100 000 neurons.
- The separation of one module from another takes place where the connectivity tends to be increasingly of a feed-forward type relative to the amount of feedback.
- The above description is referred to as binary, in the sense that the output of a neuron is a binary variable: it either emits a spike or it does not. One can alternatively introduce analog neurons, whereby the output is a spiking rate. As far as attractors are concerned these two descriptions are practically equivalent [9].
- The discretization of time is in units which are of the order of the refractory period of a neuron. Rather than enter into a detailed discussion as to whether it is the absolute or the refractory period, we shall assume that it is of the order of a few milliseconds.
- Within a discretization period neurons fire spikes at arbitrary moments, this is supposedly captured by the asynchrony which takes place on a shorter time scale, such that all N neurons can review their PSP independently within the discretization time interval [10].

Fig. 2 presents a schematic design of the network. In the diagram all connections are marked, but this is just to indicate that they are physically possible. As will be described below, the networks function perfectly well, even if a large fraction of the synaptic efficacies are randomly set to zero.

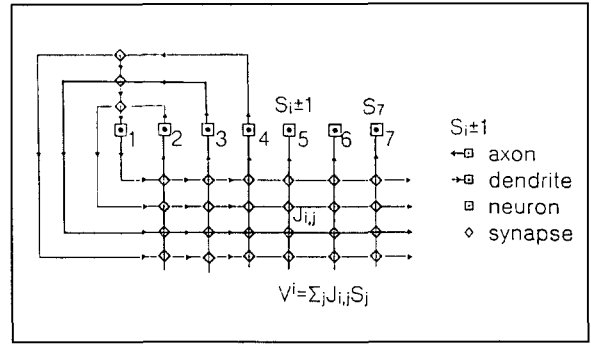


Fig. 2. Schematic design of a fully connected neural network. Squares are neural cell bodies; outgoing lines are axons; incoming lines are dendrites; diamonds are synapses.

2.2 Its dynamics

In order to describe the dynamics mentioned above one designates *network states*, which list, at any given discretization time interval, who among the neurons in the network emitted a spike and who did not. This can be done by assigning to every neuron, e.g. number j , a variable $V_j(t)$ that can take on the values 0 or 1 at the time interval starting at time t . An interval later, at $t + \delta t$, the PSP in neuron i , to be denoted by h_i , would be

$$h_i(t + \delta t) = \sum_{j=1}^N J_{ij} V_j(t). \quad (1)$$

The probability of neuron i to emit a spike at $t + \delta t$ is given by $\Pr(h_i - Th)$, where Th is the neural threshold and $\Pr(x)$ is a sigmoid centered around zero with slope of $1/T$ at zero. T parametrizes the width of the distribution which is the result of noise: high T implies high noise.

- The width T , which is the analogue of temperature in statistical mechanics [2,8], can be estimated from the average rate of spontaneous firing in a given cortical region.

Suppose that this spontaneous rate is n spikes/s; that the mean relevant refractory time is τ and that the threshold is Th , then T is the solution of the equation:

$$n \times \tau = \Pr(-Th/T). \quad (2)$$

If $n = 1/s$ and $\tau = 5ms$ then $T \approx 0.25Th$.

2.3 Associative retrieval

For a proper choice of the matrix of synaptic efficacies, such a network exhibits associative

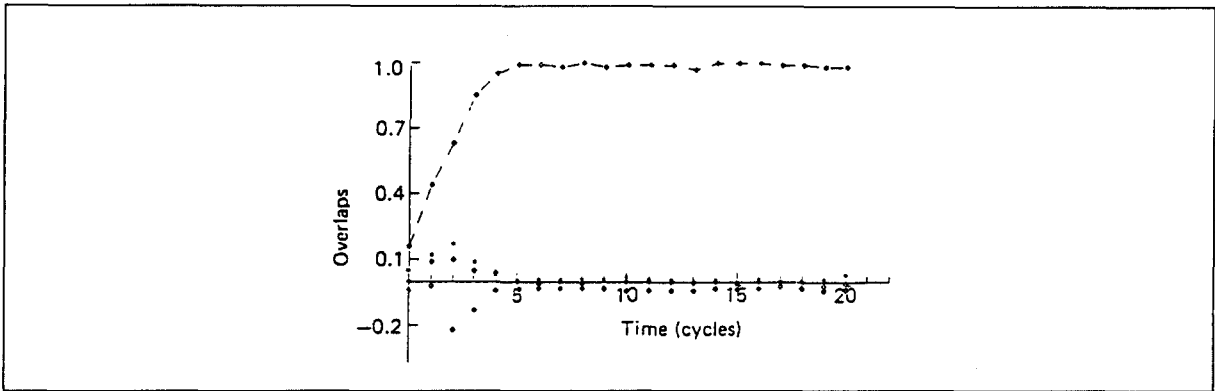


Fig. 3. Simulation of a network of 400 neurons storing 7 different patterns. The curve represents the temporal development of the similarity of the network state with the memory which resembled the stimulus most. An overlap of 1 implies that the configuration of bursting neurons is identical to a memory. The lower points are the similarity of the network state to the other stored memories. The noise parameter is $T = 0.4$ and the initial similarity is 0.16. The units on the horizontal time axis are of refractory periods.

memory in the following sense [3,11,4]:

- given an initial network state similar to one of the patterns encoded in the synapses, i.e. a distribution of firing among the neurons, or alternatively a corresponding set of weak afferent currents, and if the noise is not too high, the network states will hover in a close vicinity of the encoded pattern.

In other words, for a whole class of stimuli, not too different from one of the learned patterns, the same neurons will fire most of the time and the others will be quiescent, i.e. some of the neurons will fire bursts and the others will have very low spiking rates.

This is exemplified in Fig. 3, which shows a computer simulation of the temporal development of the similarity of the firing set of neurons to a memorized pattern, in a model neural network operating according to the dynamics described above. The network starts with a distribution of spikes with only 58% of the neurons acting (spiking or not spiking) in accordance with one of the memorized patterns. The others either spike when they should nor or do not spike when they should.¹ Associative memory is expressed in this figure by the fact that rather rapidly the similarity becomes very close to unity, which means that the correct neurons burst while the others remain mostly quiet.

The small fluctuations are due to the noise, which in this simulation is about $0.4Th$.

2.4 Attractors, synapses, storage and robustness

The bursting pattern to which the network tends is the attractor. Its particular structure, in terms of the distribution of bursts among neurons, is determined by the structure of the synaptic matrix. Early versions of the model chose very carefully designed synaptic values, constructed out of the patterns to be stored, by some process of *learning*. The patterns were chosen uncorrelated and with half of the neurons active and half quiescent. Such networks were proved to be able to store, in a single network, twice as many different patterns as there are neurons in the network [12,13]. As the level of correlation increases the storage capacity increases and becomes eventually quadratic in the number of neurons [13,14]. This should be emphasized in view of very recent statements to the contrary [15].

The early versions of synaptic matrices looked rather contrived and fragile. It was quickly appreciated that fragile they were not. It has been shown, both analytically and by simulations that the properties of the networks were rather robust under extensive disruption. It was found that one can sever *randomly* a high proportion of the synapses and affect the functioning of the network very gently. It was also found that the values of the synaptic efficacies can be clipped to a very

¹ It should be appreciated that when this figure becomes 50%, the stimulus is totally uncorrelated with the memory.

narrow set of values, without severely reducing the functioning of the system [16] (For a more extensive list of results and references see e.g. [8]).

The original Hopfield proposal for the synaptic matrix had several unrealistic features about it, which made it so fertile for quantitative study. Many of those results, concepts and intuitions survive the modifications required by reality. We shall return to a discussion of the synaptic organization in Section 3, following a discussion of another issue raised by biology.

2.5 Low burst rates – experiments and ANNs

An inspection of the findings of Miyashita and Chang discloses that the neurons whose activity becomes enhanced reach rates of 10–15 spikes/s. A systematic study of the occurrence of high rates

in a cognitively active part of the cortex was recently completed by Abeles et al. [17]. They have made extensive spike recordings in the prefrontal cortex of rhesus monkeys performing localizing tasks. While this impressive study draws the conclusion that ANN models should be disfavored, I tend to draw the opposite conclusion from the same data. The data clearly shows that in this region of cortex there are effectively no burst with rates higher than 20/s. On the other hand, the data shows that a neuron would burst at 10/s once every 10 seconds.

In fact, it seems to me, that the data of Abeles et al supports the attractor picture in yet another sense. They produce spike rasters of several simultaneously recorded neurons, to argue that bursts, when they occur, are uncorrelated between neurons. This appears to be the case for bursts of

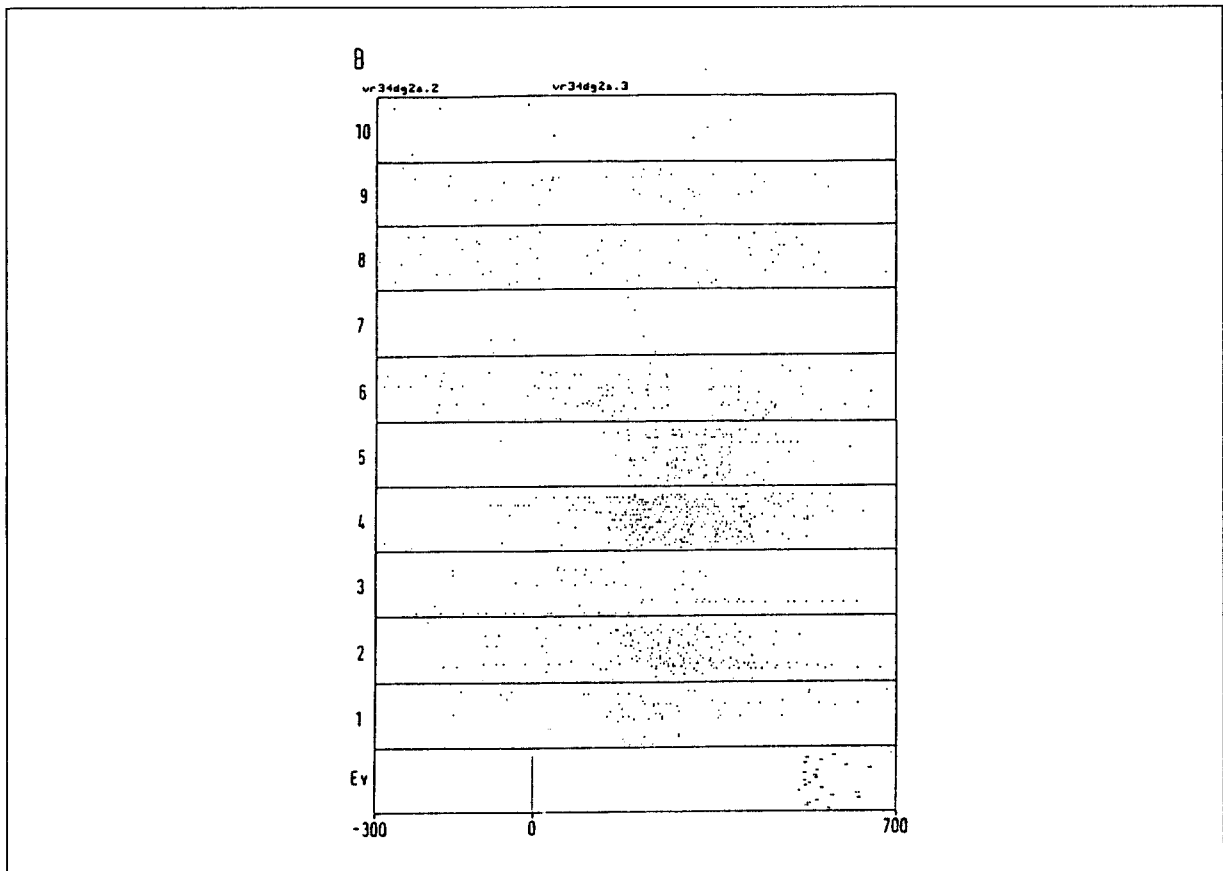


Fig. 4. Spike activity of 10 concurrently recorded neurons (1–10) in the prefrontal cortex of a performing monkey. Each panel displays the times of spikes (rasters) of one of these neurons over one second in 21 trials (each line inside a panel is a separate trial). The common time signal is the external GO signal marked O in the bottom panel, marked Ev (events in the environment). From [17].

very rare high rate. But the same rasters that demonstrate this fact, show that at the rate of 10–15/s the bursts in neighboring neurons are indeed well correlated, as one would expect in an attractor picture. Yet only the rates are correlated, not the times of the spikes.

The nature of the phenomena can be seen in a sample recording session, *Fig. 4* taken from Abeles et al. [17]. In this figure one observes the simultaneous activity of 10 neurons during a second which starts 300 milliseconds before the GO signal given to the tested monkey. I suggest that neurons 2, 4 and 5 and perhaps also 1 have correlated enhancement of their spiking rates. The spiking times in each one of the rasters looks uncorrelated with the others.

At this point one is obliged to conclude that:

- computation by bursts of high rates is ruled out, at least in associative parts of primate cortex. In some other regions, such as the parietal cortex, one does observe bursts of significantly higher rates, as high as 100–150/s [6]. One has therefore to draw a second conclusion,
- computation burst rates, and hence spike rates in attractors, vary from region to region and must be tunable.

Both conclusions pose a severe problem to early models of ANNs. The reason is that the natural rates in all attractors are intrinsically equal. Moreover, the rates must be approximately equal to the inverse of the refractory period that is built into the models, namely about 150–200/s. In addition, in these models, spiking times of neurons that are active in a memorized pattern are correlated on a

time scale of a refractory period τ . This holds equally for models of discrete and of analog neurons.

The pressure of such findings, impressed on us by Abeles, has led to a profound modification of the models. But, the modified models preserve the main conceptual framework, i.e. the computation in terms of associative attractors in the presence of dynamic noise. Two such models have been put forth, one by Amit and Treves [18] and the other by Rubin and Sompolinsky [19]. The two models have a number of features in common:

- They avoid the functional symmetry between excitation and inhibition. The computation is carried on by the excitatory neurons only.
- The neurons in the network are explicitly separated into excitatory and inhibitory neurons. This reflects the different morphology as well physiology of the two types.
- Memory is stored in the synaptic connections between excitatory neurons, reflecting the long range nature of pyramidal neurons. The role of inhibition is to control the overall level of activity in the network.
- The neurons are typically below threshold and emit spikes due to the noise in the network. The role of the synaptic connectivity between the excitatory neurons is to make neurons which are active in a pattern be closer to threshold than those which are not.
- Excitatory neurons which are active in a memory, spike stochastically. Their spiking probability is modulated by the amount of overall inhibition.

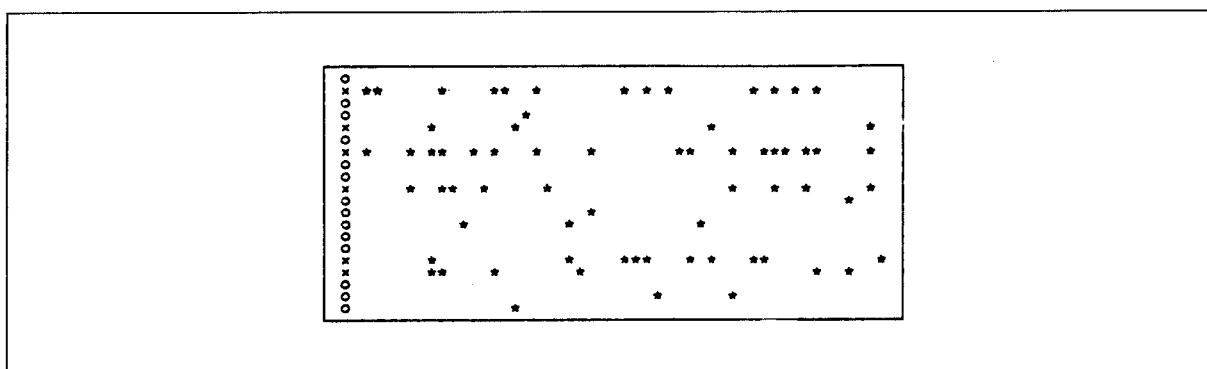


Fig. 5. Simulation of a network of 20000 neurons storing 200 different patterns. The noise parameter is $T = 0.18$. The horizontal axis extends over 50 refractory periods. The different lines are rasters of each of the 20 neurons. The column on the left indicates whether the neuron was active (x) or passive (circle) in the memorized pattern. After [18] (b).

- Neurons spike stochastically, hence spike times of different neurons active in the memory are uncorrelated. Only enhanced rates are. See e.g. the comments above concerning the findings of Abeles et al.

All these features bring the ANN models much closer to neurophysiological findings.

An example of the spiking activity of 20 randomly chosen neurons in a network of 20 000, is presented in Fig. 5. One observes that neurons which should be active in the memorized pattern have an enhanced activity rate. The others have a very low rate. The active neurons spike at uncorrelated times, but the increased rates are correlated. The rates of the active neurons are about one fifth of the maximal spike rate determined by the refractory period. This reduction in rates is controlled by a single overall parameter specifying the inhibition.

The main difference between the two models is in the prescription for the storage of the memories in the synaptic matrix. While both prescriptions for the connectivity between the excitatory neurons are naturally interpretable in terms of Hebbian learning (see below). The Rubin–Sompolinsky [19] matrix, which is constructed a la Willshaw [14] has two important advantages. First, it uses a uniform connectivity for the inhibitory input, while that of [18] has a lingering structure in these synapses, to suppresses a sensitivity to spurious attractors. The second advantage has to do with learning. It is much easier to envisage a sloppy material device, such as a synapse, that stabilizes one of two values, than one which can be modified, upon learning, in the fine way implied in [18].

3. Learning by Hebb rule and biochemistry

3.1 Reading Hebb

The Hebb rule has undergone many different interpretations, all referring to a rather simple proposal. The interpretations have served both to legitimize various synaptic model prescriptions and as strawmen for empirical attack. The literal reading of Hebb's rule is that:

- A synapse between an excitatory neuron *and any other type of neuron* is strengthened if the

spiking activity in the presynaptic neuron is followed by a spiking activity in the postsynaptic neuron.

- A synapse between an inhibitory neuron *and any other type of neuron* is strengthened if the spiking activity in the presynaptic neuron is *not* followed by a spiking in the postsynaptic neuron.

See e.g. [21] pp. 83–85.

This is a plausible description of a model interaction between two neurons. In particular, if a strong external stimulus is present persistently, each neuron affected directly by the stimulus will spike often both pre- and post-synaptically, leading to the formation of a set of synapses which will sustain the same pattern as an attractor – a reverberation in Hebb's language (op. cit. p. 110). In this picture learning a memory is tantamount to synaptic plastic modification which leads to an attractor related to the stimulus being learned. Such an attractor may be 'dug out' by persistent presentation of the stimulus, provided a Hebbian mechanism for the synaptic modification operators. Hebb admits (op. cit. p. 85) to have 'no conclusive explanation for the nature of this change'.

The essential feature of synaptic plasticity, inasmuch as it is to capture relations between afferent and efferent network activity, is that:

- the modification of a given synapse must be related to the correlation between the spiking activities of its pre- and postsynaptic neurons.

This is a necessary condition for learning. I would venture to state that empirical discovery of synaptic plasticity that does not comply with this condition, is not related to learning. The model proposed by Hebb satisfies this principle, but of course is not unique.

The reason for stressing this point is that one sometimes gets the impression that it is not fully appreciated, even in main stream neurobiology. Thus one finds, in the context of the description of an exciting research project, the statement that "Hebb's model suggests that the entire neuron participates in each storage event. Firing the postsynaptic cell...should affect most or all of the dendritic compartments" [15]². It should be ap-

² I apologize for taking up so many issues with the beautiful article of Alkon. The only reason is that it occurred as a stimulus at a particular moment.

preciated that what is attributed to Hebb is a model in which synaptic modifications are independent of the activity of the presynaptic neurons. According to the comments about learning made above, this would not be a model of learning, and no experiment concerned with learning should bother to falsify it.

3.2 Empirical proposal for postsynaptic effect

Instead, I believe, that the experiments described by Alkon are perhaps the first concrete observation which provides a biochemical basis for *bona fide* Hebb type learning, i.e. learning in which synapses are modified according to the correlation of pre- and postsynaptic spike activities, albeit mainly between excitatory neurons. It should be recalled that there has always been a theoretical problem in these types of learning schemes. It is easy to envisage, at least in principle, how the synapse 'knows' about the presynaptic spike. This is one half of the information necessary for whatever mechanism actually affects the synaptic efficacy. What has been more mysterious was the path by which information about the postsynaptic spike reaches the synapses up the dendrites, at which presynaptic activity has arrived, to form the correlation with the presynaptic activity, at those particular synapses.

The line of experiments reported by Alkon [15] involves a comparative study of the biochemical and biophysical effects of Pavlovian learning on hippocampal CA1 pyramidal neurons in a rabbit and the B-type photoreceptors of the sea snail *hermissenda*. For the sake of brevity, let us ignore here the Pavlovian aspect of the learning schedule, the justification of which I shall leave to a fuller discussion of these experiments that will be presented elsewhere.

It is observed, in both systems, that in the neural areas which are active during the learning period, there is first a generalized enhanced migration of the enzyme protein kinase C (PKC) (as well as CAM kinase II) from the cytoplasm to the membrane in the cell bodies. Later, on a scale of days, one finds that the PKC on the membranes moves to sites along the membrane of the dendrites and becomes attached to selected regions on the dendritic trees, where it remains for long durations. In the experiments the presence of these enzymes at the membrane is convincingly corre-

lated with potassium ion mobility, which in turn is related to the excitability of the membrane.

The learning scenario can therefore be as follows: suppose that the stimuli to be learned excite synapses which are on the postsynaptic neurons. Suppose further that when a group of synapses is *excitatorily* sensitized presynaptically, there is a local effect in the vicinity of such a synapse to which the migrating enzymes can attach selectively.³ Under these assumptions two problems are solved:

1. The generalized enzymatic flow affects postsynaptically those synapses which have been activated presynaptically on dendrites. This provides post synaptic input to the learning mechanism. It takes place on long time scales, as long as the persistence of the effect that binds the enzymes. The modification is dissociated from actual postsynaptic spikes.
2. If the enzymes migrates only inside neurons which have emitted spikes, then one has the required correlation of the synaptic modification with the postsynaptic spiking activity.

In other words, in the hippocampus of the rabbit some 50–60% of the neurons experience the migration of the enzymes. Those would be the neurons which emitted spikes during learning. In the other neurons in this network there was no spiking activity and consequently no enzymatic migration. The enzymes, therefore, migrate only in neurons that had been active postsynaptically, but they attach only at sites at which synapses have been sensitized presynaptically. It may be the case that in order to prolong sufficiently the time span in which the sensitized synapses can preserve the signal which allows for the attachment of the enzymes one has to rely on nonlinear effects of localization, which are strongly advocated by Alkon. Those do not change the logic of the above arguments and are not required in order to increase storage.

Acknowledgements

I am most grateful to Prof. M. Abeles for permitting me to discuss and present his findings

³ Note the different assumptions made by Alkon [15], in order to resolve a nonexistent storage problem.

prior to publication. This work was supported in part by a grant from the US-Israel Binational Science Foundation.

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