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A MODEL FOR MEMORY IN THE BRAIN

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16. Abstract

Among the many different types of memory models proposed over the past 100 years, the oldest and most persistent hypothesis has been that memory results from modification of synaptic junctions. The model proposed in this paper is a synaptic junction model which differs only slightly from other synaptic junction models, but the difference is critical. This model, like most others, suggests that facilitation of synapses is caused by coincidence of pre- and post-synaptic activity. But, unlike others, this model distinguishes between synapses in nonspecific and specific neural pathways and postulates that facilitatable memory synapses exist primarily at sites where nonspecific fibers terminate on specific pathways.

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INTRODUCTION

The residing place of memory in the brain has been one of the most elusive mysteries in the history of modern science. Memory seems to be everywhere in the brain and at the same time nowhere. Experiments to isolate it physiologically have been notable for their failure to do so. Models to explain it psychologically have been largely unable to account for important behavioral phenomena.

Among the many different types of memory models (1) proposed over the past 100 years, the oldest and most persistent hypothesis has been that memory results from modification of synaptic junctions (2). The model proposed in this paper is a synaptic junction model which differs only slightly from other synaptic junction models, but the difference is critical. This model, like most others, suggests that facilitation of synapses is caused by coincidence of pre- and post-synaptic activity. But, unlike others, this model distinguishes between synapses in nonspecific and specific neural pathways and postulates that facilitatable memory synapses exist primarily at sites where nonspecific fibers terminate on specific pathways. The implications of this distinction should become clear as we explore the details of the model and its capacity to account for various memory phenomena.

BASIC MODEL

Consider the simplified nerve cell model shown in Figure 1 which has a specific input fiber labeled IN and a specific output fiber labeled OUT. The IN fiber makes a strong synapse on the cell so that each time IN fires, the cell fires. The cell also has two nonspecific input fibers labeled x and y. The synapse of fiber x has two states, q_0 and q_1. In state q_0, the firing of fiber x has no effect on the cell. In state q_1, the firing of fiber x causes the cell to fire. The input fiber labeled y does not affect the cell itself but instead interacts presynaptically with fiber x. Firing fiber y

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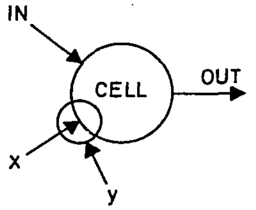


STATE OF X FIBER	y	IN	x	OUT	NEW STATE OF X FIBER
q_0	0	0	0	0	q_0
q_0	0	0	1	0	q_0
q_0	0	1	0	1	q_0
q_0	0	1	1	1	q_0
q_0	1	0	0	0	q_0
q_0	1	0	1	0	q_0
q_0	1	1	0	1	q_0
q_0	①	1	①	①	q_1
q_1	0	0	0	0	q_1
q_1	0	0	1	1	q_1
q_1	0	1	0	1	q_1
q_1	0	1	1	1	q_1
q_1	1	0	0	0	q_1
q_1	1	0	1	1	q_1
q_1	1	1	0	1	q_1
q_1	1	1	1	1	q_1

CHANGE OF STATE CONDITION

Figure 1–Basic memory cell. Truth table shows behavior under all conditions. IN fiber always fires cell; x fiber fires cell if x synapse is in q_1 state; y fiber enables x to change from state q_0 to q_1.

enables the synapse of fiber x to change states. We define the synapse of fiber x to be originally in state q_0 and be set to stage q_1 when there is a three-way coincidence between fiber-x firing, the cell firing, and fiber-y firing. A slightly more complicated version of this basic cell is shown in Figure 2. This second cell has many x-fiber inputs, $x_1, x_2, \ldots x_n$. Each of these x fibers has the same properties attributed to the single x fiber of Figure 1.

We now construct a plane of these cells as shown in Figure 3 such that all the IN fibers arrive in a bundle from the rear and all the OUT fibers exit the front. The IN fibers synapse in a strong 1:1 fashion on the cells, so this plane can be thought of as a synaptic relay station for a nerve bundle transmitting data from one point to another. We may bring the nonspecific x_1 fibers from all the cells in the plane together into a single fiber labeled X_1 and all the nonspecific y fibers into a single fiber labeled Y.

Assume all the x_1 synapses are originally in the q_0 state. If the IN fibers are now excited in some pattern A, the OUT fibers will transmit the A with no loss. We use the A pattern for illustrative purposes only. We do not mean to imply that the IN fibers carry an unprocessed retinal image. The A instead represents highly processed data from feature extractors which precede the memory planes in the sensory pathways.

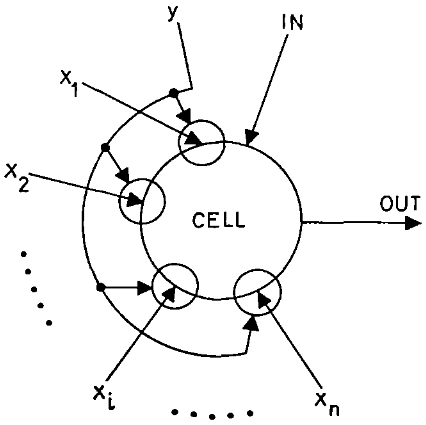


Figure 2–Basic memory cell with many variable x-fiber synapses.

If the X_1 and/or Y fiber is fired when nothing is coming in on the IN fibers, there will be no output because all the x synapses are in the original q_0 state. If, however, while the A is on the IN fibers, the Y fiber and the X_1 fiber are fired, all the x_1 fiber synapses attached to cells which are firing will be set to the q_1 state. All other x-fiber synapses will be left in the q_0 state. The A pattern, of course, appears on the OUT fibers just as it would if the Y and X_1 fibers had not been fired. However, the firing of the Y and X_1 fibers in coincidence with the A pattern on the IN fibers has caused the A pattern to become imprinted on the x_1

synapses. If at a later time the X_1 fiber is fired, all the x_1 synapses set to the q_1 state by the A pattern will fire cells, and the OUT fibers will emit the A pattern even though nothing is coming in on the IN fibers.

In a similar way, if pattern B occurs in association (or in coincidence) with Y and X_2 firing, pattern C in association with Y and X_3 firing, etc., then pattern B can later be elicited by firing X_2, pattern C by firing X_3, etc. We thus have a model for a form of associative memory (3) where A, B, C, etc., are the incoming patterns, and X_1, X_2, X_3, etc., are the associated states of the brain, or the context.

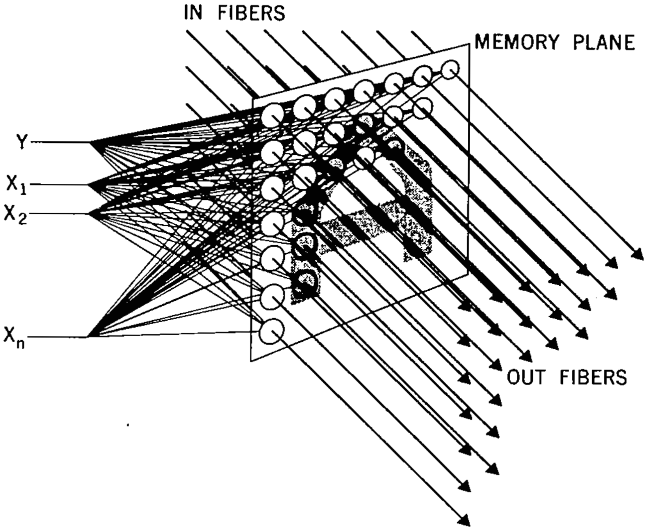


Figure 3–Memory plane made up of many memory cells of the type shown in Figure 2.

The nonspecific Y fiber carries the memory enable signal which can be postulated to be a motivational influence. If the Y fibers are not activated, the x synapses will not change states and memory will not be stored (or consolidated).

To give a simple layman's example of the operation of this model for associative memory, let us assume that the smell of a particular exotic perfume causes the firing of certain nonspecific x fibers in the visual association areas. If at the same time the eyes are viewing a particular voluptuous female, feature extractors in the visual pathways will also be sending signals to the same visual association area via specific IN fibers. If one's motivation is such that one's y fibers are excited, this pattern of visual features from the IN fibers will then become imprinted on the nonspecific x synapses which are activated by the olfactory system. At some later date, recall of the visual features of the same voluptuous female will thus be elicited by the smell of the same exotic perfume.

Read-In Mechanisms

This memory model allows a reasonable physiological mechanism for read-in of both long-term and short-term memory. Referring to Figure 4, suppose that the firing of an x fiber releases transmitter substance S_1 into the synaptic cleft which produces an excitatory postsynaptic potential in the cell dendrite. Suppose further that whenever the cell fires, it releases substance S_2 (such as K+ ions) into the same area. Now the presence of S_1 and S_2 at the same time in the synaptic cleft means a coincidence has just occurred between the cell firing and the x-fiber firing. If S_1 and S_2 combine to form S_3 which acts on the synaptic endplate to facilitate it temporarily, we have a mechanism which produces short-term memory. The decay of S_3 would cause decay in short-term

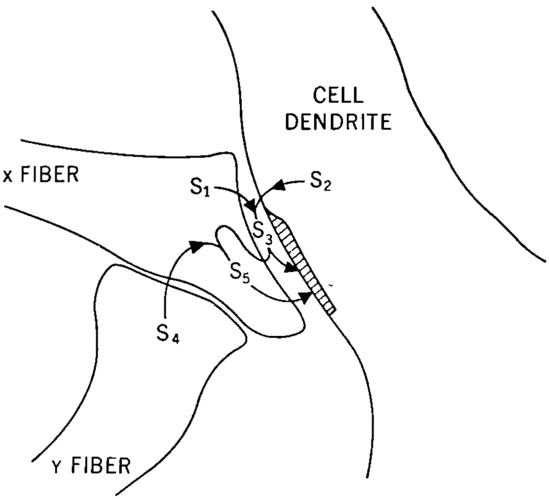


Figure 4–Hypothetical microstructure for the variable x synapses on a memory cell. S_1, S_2, S_5 indicate transmitter chemicals released or produced during fiber and cell firings.

memory. Now assume that firing the y fiber releases another substance, S_4, into the presynaptic knob of the x fiber and, perhaps also, into the synaptic cleft. If before S_3 decays, it comes into contact with S_4, it reacts to form S_5 which in some way effects a permanent facilitation of the x synapse, perhaps by enlarging the endplate or the synaptic knob or both. This is the process of consolidation of long-term memory.

Memory consolidation by these mechanisms could be inhibited by drugs which inhibit the action of S_4 or S_5 or which inhibit the synthesis of protein. Memory consolidation could also be prevented by destruction of y fibers by surgical means. The reported loss of capacity to consolidate memory caused by lesions in the hippocampal areas (4) suggests that y fibers may originate in the hippocampus. Full-memory consolidation could also be prevented by a convulsive shock producing a flood of impulses which would severely degrade the remembered pattern by flooding all the x-synapses with S_5. Retroactive inhibition would be caused by similar but less massive overwriting of the x synapses.

Our model thus provides a simple and natural explanation for many of the phenomena related to associativity, decay in short-term memory, and consolidation of long-term memory. It is necessary, however, to back off somewhat from the oversimplification of an x synapse assumed to have only two states. We can more reasonably assume that the x synapse is continuously variable in the range between q_0 and q_1 and is subject to all the foibles customarily attributed to synapses. We also cannot suppose that a single coincidence is sufficient to set an x synapse to the q_1 state; repeated coincidences would be necessary to firmly imprint an image permanently on a memory plane. Thus each coincidence merely increments the synapse toward the q_1 state. The number of coincidences required for imprinting may vary for memory planes in different parts of the brain. Thus one-trial learning may be possible at some levels but not at all. In addition, we need not insist that each X fiber is connected to every cell in the memory plane. Connection of a given X fiber to various cells scattered randomly over the plane would produce a similar effect. Random connections and probabilistic firings produce a property that one might call vividness of memory. We can define the vividness of memory as the extent to which the memory-evoked pattern resembles the original pattern. The vividness of a memory will depend on whether all the x synapses associated with that memory are sufficiently strong to fire reliably and also on whether exactly the same X fibers fire at the recall time as fired at imprinting time.

It is not clear whether it is necessary to provide the model with a mechanism for resetting the x fibers to the q_0 state. There is some controversy as to whether, once memory is consolidated, forgetting is caused by decay of the memory trace or by interference in some manner similar to that of retroactive inhibition. In the former case, the model could assume that the synapse of an x fiber which was seldom fired would slowly atrophy back to the q_0 state. In the latter case, the model would need no resetting mechanism.

As a Model for Discrimination Learning

Let us consider how this model of memory might be applied to a classical conditioning situation. Assume that we pair the visual pattern of a horizontal bar with food and that of a vertical bar with an electric shock, as diagrammed in Figure 5. The unconditioned stimulus of food causes eating activity; the shock causes fleeing. When the horizontal bar is presented, a signal is put out on X_1. If food arrives while this signal is present, the taste of food will be imprinted on memory plane M_1 and nothing will happen to M_2. When the vertical bar is presented, a signal appears on X_2. If electric shock arrives while the signal is present, the pain of shock will be imprinted on memory plane M_2 and nothing will happen to M_1. Thereafter, presentation of the horizontal bar will elicit eating responses and presentation of the vertical bar will elicit fleeing responses. Note that presenting the conditioned stimulus after the unconditioned stimulus has passed (backward association) produces no conditioning. The situation in which the bar stimulus is removed before the unconditioned stimulus is given can be handled by requiring that the pattern recognizers recognize the sequence "bar followed by pause" before emitting X_1 or X_2. (One could alternatively assume that substance S_1 lingers in the synaptic cleft for some time after the X firings cease.) The speed of learning will depend in large measure on the level of activity of the nonspecific Y inputs, which is controlled by the motivational level of the animal. This level can be raised by either reward or punishment and will be influenced also by fatigue and by various drives such as hunger and thirst.

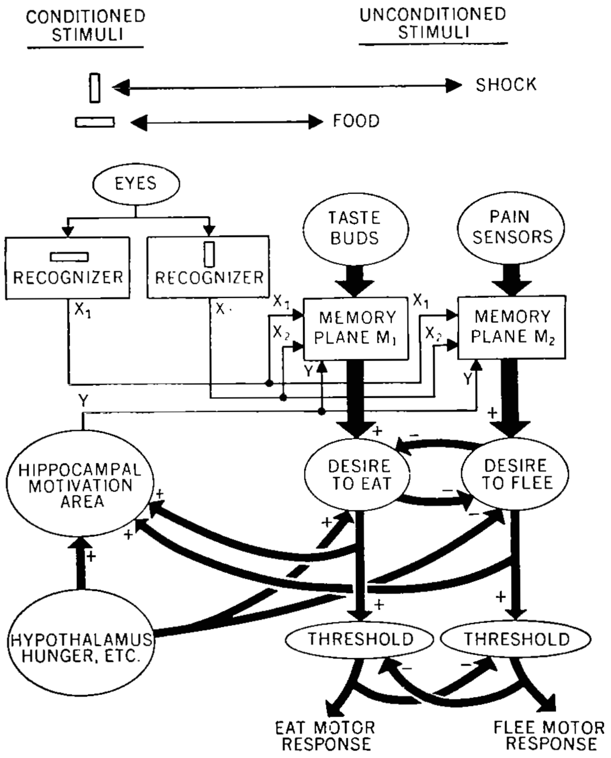


Figure 5–A model of the complete system responsible for classical conditioning. The + and − signs on arrowheads indicate excitatory and inhibitory influences respectively.

This same model also produces the proper responses to Type-2 conditioning, or instrumental learning situations. Assume that the horizontal and vertical patterns are on bars which the animal can press. Pressing the horizontal bar results in food; pressing the vertical bar results in shock. Before the initial bar-pressing, the Y-inputs will have some low level of activity. After the first bar-pressing experience, the Y inputs will increase at a rate depending on the strength of the reward or punishment and on the state of the internal drives. Seeing the horizontal bar and pressing it causes an X_1 signal to be present. When the Y levels are sufficiently high, the food resulting from bar-pressing becomes imprinted on plane M_1. Similarly, the shock becomes imprinted on plane M_2.

After learning has occurred, the animal will, upon seeing the horizontal bar, receive a suggestion of food from the x_1 synapses in plane M_1. If he approaches the horizontal bar, he will make the X_1 signal stronger. This will increase the vividness of the suggestion of food. If he behaves so as to maximize the vividness of the suggestion of food, he will actually press the bar. Of course, during this period, the suggestion of food has raised the Y activity to a very high level. Hence, with every bar-pressing and food-reward cycle, the x_1 synapses in M_1 become more firmly imprinted with the food experience.

Note that variable learning rates and abilities can be accounted for with this model by adjustment of parameters in the system as noise, effectiveness of the chemical substances, number of variable synapses, sophistication of the sensory data filters, etc.

This oversimplified model of discrimination learning illustrates a fundamental problem of data storage and retrieval in the conditioning process. The model requires specific preprocessing of sensory data before its arrival at the memory sites. In this example, the bar recognizers may correspond to groups of complex and hypercomplex cells such as have been observed by Hubel and Wiesel (5), and many others. This is a critical point because without presupposing such pattern recognizers, this model cannot explain the learning process. This implies that structure exists before learning. Such an assumption is consistent with other current work in this field. Although the notion of learning taking place in a completely random net of interconnected cells has been widely proposed by Hebb (2) and others, no very powerful memory structure has ever derived from these conjectures. Rosenblatt's work (6) with the randomly connected "Perceptron" lent some support to the concept of learning in random nets, but recent, more careful analysis of perceptron-learning theory has led Minsky (7) to the conviction that "significant learning at a significant rate presupposes some significant prior structure."

As a Motor-Command Sequence Generator

The problem of generating output motor responses is one of great complexity. Motor activity requires two fundamental processes: first, the generation of complicated sequences of commands;

second, feedback control which compares or correlates incoming patterns with stored patterns and generates commands for corrective motor activity to decrease the discrepencies. Both processes involve memory storage and recall. The model presented here is capable of producing both functions in a natural and straightforward way.

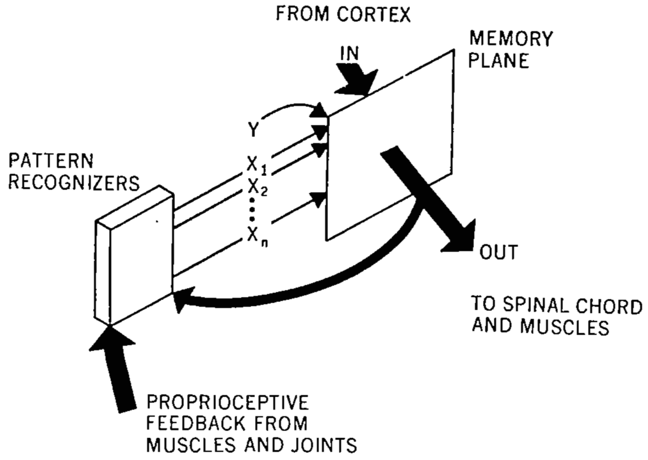


Figure 6–A system for generating or regulating sequences of motor commands.

Consider a memory plane like that of Figure 6. Suppose at some time t_0, the initial command A in the command sequence ABCD. . ., passes through this memory plane on its way from the motor cortex to the spinal cord. Suppose, also at t_0, that proprioceptive feedback signals from the muscles and joints in their initial t_0 position are being received and recognized by the pattern recognizers, producing the X_1 signal. The X_1 signal along with the Y input will then imprint the initial command, A on the X_1 synapses. In response to the A command, the muscles and joints now move to a new position, causing the pattern recognizers to output X_2. If at this time command B is sent from the cortex, it will be imprinted on the x_2 synapses. This process may continue for a lengthy sequence of cortex motor commands ABCD . . . and resulting body position responses $X_1X_2X_3$. . . . Upon repetition of the sequence of motor commands, the signals from the cortex will be reinforced by the output from the imprinted x synapses. In turn, the x synapses will be strengthened by the repetition of the sequence. Upon each repetition, more and more of the muscle control can be assumed by the output from the x synapses, and less attention is required by the cortex.

When learning is complete, the sequence of motor commands, A B C D E. . ., can be elicited entirely from the memory plane via the X_1 X_2 X_3 . . . sequence inputs without control from the cortex except perhaps to initiate and/or terminate the sequence by some means which is not specified in this simple model. It is tempting to speculate that this type of circuit makes up the bulk of the cerebellum. However, such sequence generators are likely also to be located at many other levels in the motor pathways. It is possible for sequence generators of this type to be arranged in a hierarchy. For example, consider the structure of sequences shown in Figure 7.

The motor cortex generates the command sequence I, II, III, ... The caudate nucleus is triggered by these commands and generates a sequence of subcommands 1, 2, 3, 4, . . . , and so on at the cerebellum and spinal-chord levels. At each level, sequences are cycled by feedback from

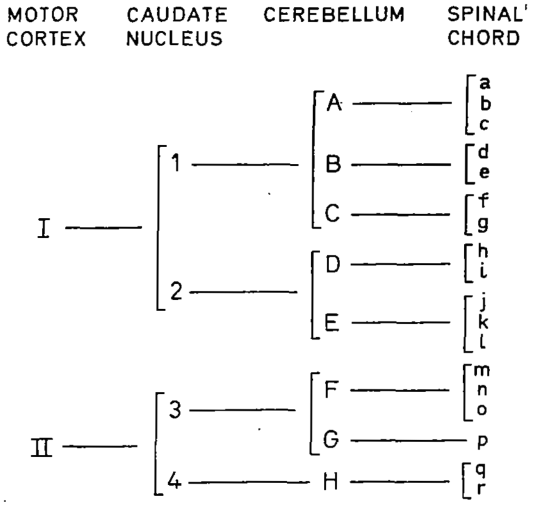
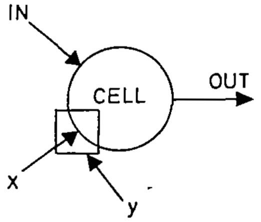


Figure 7–A possible hierarchical arrangement of sequence generators in the motor system.



STATE OF x FIBER	y	IN	x	OUT	NEW STATE OF x FIBER
q_0	0	0	0	0	q_0
q_0	0	0	1	0	q_0
q_0	0	1	0	1	q_0
q_0	0	1	1	1	q_0
q_0	1	0	0	0	q_0
q_0	1	0	1	0	q_0
q_0	1	1	0	1	q_0
q_0	①	1	①	①	q_1 CHANGE OF STATE CONDITION
q_1	0	0	0	0	q_1
q_1	0	0	1	0	q_1
q_1	0	1	0	1	q_1
q_1	0	1	1	0	q_1
q_1	1	0	0	0	q_1
q_1	1	0	1	0	q_1
q_1	1	1	0	1	q_1
q_1	1	1	1	0	q_1

Figure 8–A basic memory cell with an inhibitory variable x synapse. When the synapse is in the q_1 state, the x fiber can inhibit the cell from firing.

below and are initiated or terminated by commands from above. It is not necessary that this feedback come entirely from the proprioceptors. Shorter feedback paths are possible to account for extremely rapid sequences. Different degrees of plasticity in the x synapses may exist at the various levels. For example, in the spinal chord, most of the x synapses may be genetically "hard-wired" and not capable of changing state; whereas, in the motor cortex, caudate, and cerebellum, most or all of the x synapses may be variable. Animals and insects whose memory planes contained mostly or entirely genetically hard-wired x synapses would have instinct-dominated behavior patterns. However, a single plane of variable synapses anywhere in the stimulus-response pathway would provide a site for some conditioning. Evidence for genetically hard-wired sequence generators is common among studies of insect behavior.

As a Pattern Correlation Detector

A modification of the memory plane will produce a different kind of plane which measures the correlation between new patterns and stored patterns. For clarity, let us call the type of memory plane which we have discussed up to this point a Type-1 plane. The modified plane we will now discuss, we will call Type 2.

Consider a second kind of cell as shown in Figure 8. With this cell, the x-fiber synapse again has two states, q_0 and q_1. State q_0 is identical with q_0 for the cell in Figure 1. In this case, however, when x is in state q_1, a pulse on x will inhibit the cell from firing in response to a pulse on IN. A plane of such cells can imprint a pattern A as before. However, now when X_1 is fired, all cells within the imprinted pattern are inhibited. Thus if A is imprinted on the

x_1 synapses in the plane and A* is put on the IN fibers, when X_1 is fired, only the * will appear on the OUT fibers. If we define A^0 as the pattern imprinted on the x synapses and A^N as the pattern presently on the IN fibers, the memory plane will produce $A^N - A^0$ on the OUT fibers when X_1 is fired. It is possible to obtain all possible Boolean functions of A^N and A^0 by introducing planes made up of cells which make point-to-point comparisons between the two types of memory planes. Cells to generate Boolean functions (8) are shown in Figure 9.

Figure 10 shows two more planes of cells arranged so as to generate the functions A^0 and $A^0 - A^N$. A summation of all the cells firing in the two planes producing $A^N - A^0$ and $A^0 - A^N$ provides a null when $A^N = A^0$. Thus we have a measure of the correlation between A^N and A^0.

The ability of memory to correlate incoming patterns with stored patterns and to generate error signals when the two differ is a critical function for the regulation of any sort of goal-directed behavior. This type of pattern recognition is also critical to the parsing of written or spoken language. Indeed, it is critical to the formation by a creature of any kind of internal representation of the external environment.

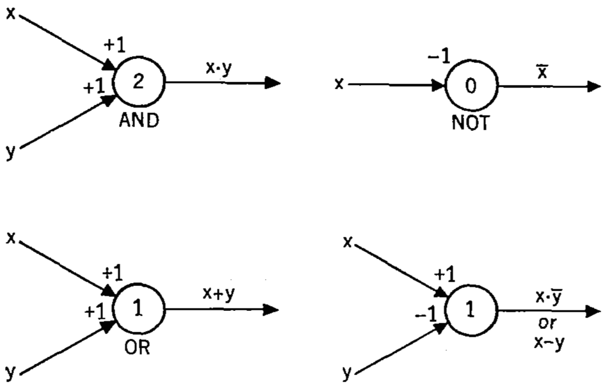


Figure 9—McCulloch-Pitts type cells capable of generating Boolean functions of two variables. A cell fires if the sum of active inputs equals or exceeds the threshold value printed inside the cell.

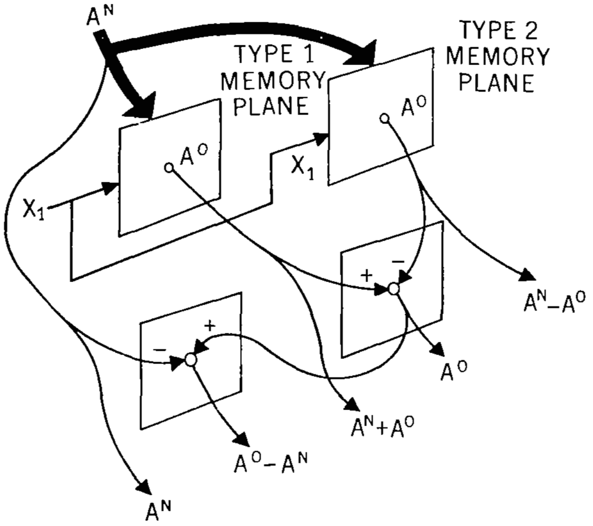


Figure 10—A network capable of computing various comparisons between incoming patterns and stored patterns.

The form of the memory planes and their pattern recognition capabilities suggest that they might be interconnected in a web or graph structure so as to store data in a contextual or relational way. Information storage and retrevial in such a structure, where relationships between patterns constitute the storage and recall mechanisms, could be the basis for what we call intelligence (9). This possibility has recently been explored (10).

Objections

An objection to this model of memory might be raised on the grounds that it is eidetic, or template matching – that is, it records and later reproduces each pattern exactly as it occurs on the memory plane, without allowing for size or position transformations. For example, a new A would not be recognized as similar to a stored A unless the two A's matched closely in size and position on the memory plane.

There are two answers to this objection. First, eidetic memory is known to exist in the brain, at least in some individuals (11). Second, and much more to the point, there is no reason to require the memory mechanism itself to produce size or position invariance. One need not suppose that the information to be remembered is presented to the memory in the form of a retinal image which moves and changes size, yet retains the same information. It is much more likely that the data to be stored is highly processed. The inputs to memory planes are probably, in most cases, the outputs of feature extractors. If this is the case, it would be most undesirable for the memory plane itself to behave in any other but an eidetic manner. Otherwise, one would be likely to store information about vertical lines and later retrieve information about red spots. The nervous system has mechanisms for performing many types of transformations on raw sensory data, including size and position invariant transformations. It is quite conceivable that memory planes play some role in the performance of these transformations. However, it is both unnecessary and unlikely that memory units themselves exhibit any transformational invariance.

Another possible objection to the model might be that unrealistic requirements are placed on the pattern recognizers which output the X fibers. In the simple Type 1 and Type 2 memory planes discussed, each X-fiber must exclusively represent a particular combination of patterns inputed to the pattern recognizer. The combinatorics of this requirement lead to an absurd number of X fibers required for any reasonably versatile memory. However, it is quite likely that memory planes in the brain consist of cells with both Type 1 excitatory and Type 2 inhibitory x-fiber synapses on the same cells. This interplay of excitatory and inhibitory influences makes it feasible for a particular X-fiber firing to represent the occurrence of a particular input pattern instead of a particular combination of input patterns. A very large number of X-fibers are still required in order to implement a complex memory, but the number seems at least to be within the bounds of the number of cells known to exist in the brain.

Anatomical Evidence

Let us now examine the rather striking similarity between the structure of this memory model and the anatomical structure of the cerebellum.

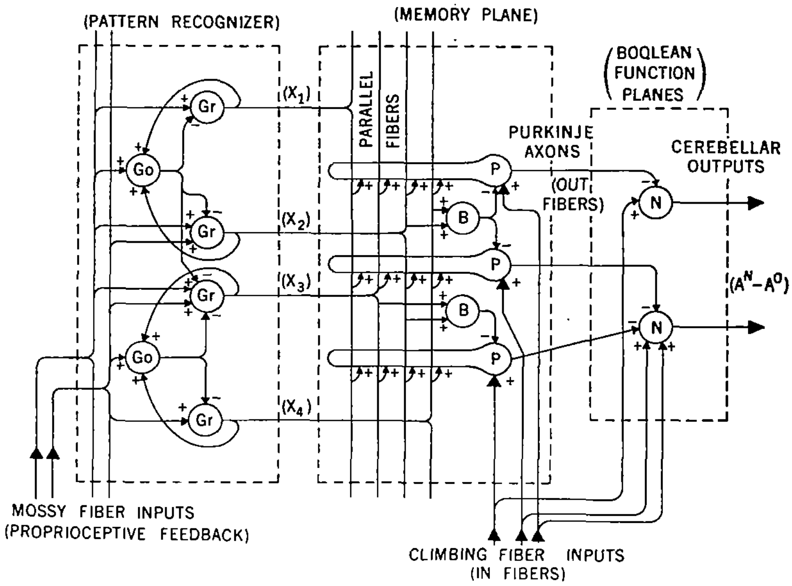


Figure 11–Diagram of cerebellum showing correspondence between memory model and anatomical structure of cerebellum. Wiring schematic of cerebellum is constructed from Eccles' description of synaptic connections in the cerebellum (13). Memory model correlates to cerebellar structure are enclosed in parentheses: Gr, Granule cells; P, Purkinje cells; B, Basket cells; N, Nuclear cells; Go, Golgi cells.

The structure of the cerebellar cortex has been carefully investigated by many competent anatomists and physiologists (12, 13). The cortical structure is quite uniform throughout the cerebellum and is also relatively simple. There are only five types of cerebellar cortex cells: (1) Purkinje cells, (2) Basket cells, (3) Granule cells, (4) Golgi cells, and (5) Stellate cells. These cells are arranged in three layers. There are only two types of input fibers to the cerebellar cortex: mossy fibers and climbing fibers – and there is only one type of output fiber, the Purkinje axons.

A great deal is known about the types of fiber connections and synaptic interactions in the cerebellum, due to recent work by Eccles, Ito, and Szentagothai (14). The climbing fiber inputs enter the cerebellar cortex and each climbing fiber synapses with a single Purkinje cell in a 1:1 relationship. This arrangement suggests that the climbing fibers of the cerebellum correspond to the IN fibers of the model while the Purkinje axons of the cerebellum correspond to the OUT fibers of the model. These analogies are illustrated in Figure 11.

The mossy fiber inputs to the cerebellum are entirely different. These fibers arborize over a wide region making excitatory synaptic contacts with up to 200 widely scattered granule cells.

Each granule cell receives inputs from about five different mossy fibers. When a pattern of impulses arrives on the mossy fibers, some granule cells receive several excitatory inputs; others receive few or none. Any granule cell excited above threshold will fire, sending impulses out on its axon. Axons from these granule cells form a layer known as the parallel fibers.

Golgi cells sample parallel fiber activity from granule cells in their vicinity. When this activity rises too high, the Golgi cells feed back inhibitory pulses to a large number - about 100,000 granule cells in this vicinity. This feedback arrangement tends to allow only the most strongly excited granule cells in any region to fire. We thus hypothesize that specific input patterns on mossy fibers are decoded into specific firings of widely spaced granule cells. If indeed this is the case, the granule cell axons strongly resemble the X fibers of the memory plane.

This interpretation requires an extremely large number of granule cells. The granule cells are, however, the most numerous cells in the brain. It is estimated (13) that there are 3×10^{10} granule cells in the cerebellum alone.

The hypothesis of widely spaced granule cell firings is contrary to a widely held belief that the cerebellum functions by granule cells firing in closely packed groups, so as to give rise to "beams" of parallel fiber firings. Our model predicts that in order for the cerebellum to regulate motor activity, the parallel fibers need not fire in beams in a conscious, active animal and in fact, probably do not. This prediction is subject to experimental verification.

The axons of the granule cells, parallel fibers, spread throughout the dendritic trees of the Purkinje cells. Each parallel fiber makes excitatory synaptic contacts with about 300 different Purkinje cells. These synapses rather closely resemble the excitatory x synapses in our model. In addition, each parallel fiber makes excitatory contacts with up to 300 Basket cells and also a number of Stellate cells. Each Basket cell in turn makes inhibitory synapses with about 50 Purkinje cells. The Stellate cells make inhibitory contacts with perhaps several hundred Purkinje cells. This combination is reminiscent of the inhibitory x synapses (Type 2) in the memory model. Whether these nonspecific excitatory and inhibitory synapses in the cerebellum are of the variable type is of course not known.

The outputs from the Purkinje cells leave the cerebellar cortex and most of them form inhibitory synapses on nuclear cells in the intracerebellar nucleus and the Deiters nucleus. The climbing fibers also make excitatory synapses of these same nuclear cells. Thus the cerebellum as a whole seems to resemble very closely to a configuration of the type suggested in Figure 10.

In our analysis of the cerebellum, we have not found any cerebellar correlate for the motivational y inputs of the model. However, it is possible that there are no motivational inputs to learning in the cerebellum; cerebellar learning may well be confined to motor sequences which are learned only by repetition, irrespective of motivational influences.

Much less is known about the specific behavior of and the connections between cells in most other areas of the brain. However, there is a clear distinction between large cells (macroneurons), such as pyramidal cells with large dendritic fields and axons which transmit over long distances; and small cells (microneurons), such as Golgi Type-2 neurons whose axons branch extensively and synapse with a large number of other cells in a restricted neighborhood. This extensive branching has for many years been thought to be directly related to intelligence in general, and memory in particular (15).

Recent theoretical studies of the structure and function of the cerebellum have expanded and refined this basic cerebellar model. Specifically, the pattern recognizers shown in Figures 6 and 11 have been explored in detail and an algorithm for adjusting synaptic strengths has been suggested (16).

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