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Functions of Neuronal Networks in the Hippocampus and Neocortex in Memory

Edmund T. Rolls

I. Functions of the Primate Hippocampus in Memory

It is known that damage to certain regions of the temporal lobe in humans produces anterograde amnesia evident as a major deficit following the damage in learning to recognize new stimuli (Scoville and Milner, 1957; Milner, 1972; Squire, 1986; this volume, Chapter 12). The anterograde amnesia has been attributed to damage to the hippocampus, which is within the temporal lobe, and to its associated pathways such as the fornix (Scoville and Milner, 1957; Milner, 1972; Gaffan, 1974, 1977), but this has been questioned, and instead it has been suggested that damage to both the hippocampus and the amygdala is crucial in producing anterograde amnesia, in that combined but not separate damage to the hippocampus and amygdala produced severe difficulty with visual and tactual recognition tasks in the monkey (Mishkin, 1978, 1989, 1982; Murray and Mishkin, 1984, 1985). In investigations of the particular aspects of memory for which the hippocampus may be essential, it has been shown that monkeys with damage to the hippocampo-fornical system have a learning deficit on memory tasks that require them to make associations between a stimulus—for example, a picture—and a spatial motor response such as touching one part of a screen (Gaffan, 1985; Rupniak and Gaffan, 1987), and are also impaired on memory tasks that require combinations of stimulus attributes with their locations in space to be processed together, such as memory not only for which object was shown but where it was shown (Gaffan and Saunders, 1985). Further, humans with right temporal-lobe damage are also impaired in conditional spatial response and object-place memory tasks (Petrides, 1985; Smith and Milner, 1981).

campus in memory, the activity of 1510 single hippocampal neurons was recorded in rhesus monkeys learning and performing these memory tasks known to be impaired by damage to the hippocampus or fornix (Rolls *et al.*, 1989; Miyashita *et al.*, 1989; Cahusac *et al.*, 1989).

In an object-place memory task in which the monkey had to remember not only which object had been seen in the previous 7–15 trials but also the position in which it had appeared on a video monitor, neurons were found that responded differentially depending on which place on the monitor screen objects were shown (Rolls *et al.*, 1989). These neurons comprised 9.4% of the population recorded. It is notable that these neurons responded to particular positions in space (whereas “place” cells in the rat respond when the rat is in a particular place; O’Keefe, 1983). In addition, 2.4% of neurons responded more to a stimulus the first time it was shown in a particular position than the second time. These neurons thus responded to a combination of information about the stimulus being shown and about position in space, for only by responding to a combination of this information could the neurons respond only when a stimulus was shown for the first time in a certain position in space.

In tasks in which the monkeys had to acquire associations between visual stimuli and spatial responses, 14.2% of the neurons responded to particular combinations of stimuli and responses (Miyashita *et al.*, 1989). For example, in a task in which the monkey had to perform one response (touching a screen three times) when one visual stimulus was shown, but had to perform a withholding response for 3 sec to obtain reward when a different stimulus was shown (Gaffan, 1985), 9.2% of the neurons responded to one of the stimuli if it was linked to one of the responses in this task. The same neurons typically did not respond if the same stimuli or the same responses were used in different tasks, or if other stimuli were associated with the same responses in this task. Thus these neurons responded to a combination of a particular stimulus with a particular spatial motor response (Miyashita *et al.*, 1988).

It was possible to study the activity of 41 hippocampal neurons while the monkeys learned new associations between visual stimuli and spatial responses. In some cases it was possible to show that the activity of these neurons became modified during this learning (Cahusac *et al.*, 1986, 1989). Interestingly, 33% of the neurons that altered their responses during this learning showed a sustained differential response, but 67% of the neurons differentiated between the stimuli only at or just before the monkey learned the task, and stopped differentiating after 5–10 more trials. This is consistent with the possibility discussed below that the neurons that show large sustained differential responses inhibit the other neurons that show transient modification, so that as a result of competition not all neurons are allocated to one stimulus-spatial response association.

responses related to certain types of memory. One type of memory involves complex conjunctions of environmental information—for example, when information about position in space (perhaps reflecting information from the parietal cortex) must be memorized in conjunction with what that object is (perhaps reflecting information from the temporal lobe visual areas), so that where a particular object was seen in space can be remembered. The hippocampus is ideally placed anatomically for detecting such conjunctions, in that it receives highly processed information from association areas such as the parietal cortex (conveying information about position in space), the inferior temporal visual cortex (conveying a visual specification of an object), and the superior temporal cortex (conveying an auditory specification of a stimulus) (Van Hoesen, 1982) (see Fig. 5). The positions of stimuli in space may be represented by the firing of hippocampal neurons as described above so that conjunctions of, for example, objects and their position can be formed. It is also suggested that one neurophysiological mechanism by which “place” cells in the rat (see O’Keefe, 1983) may be formed is by conjunction learning of sets of simultaneously occurring stimuli in different parts of space, each set of which defines a place.

II. Computational Theory of the Hippocampus

A possible theoretical basis for these results, and in particular how the hippocampus may perform the conjunction or combination learning just described, is now considered.

A schematic diagram of the connections of the hippocampus is shown in Fig. 1. One feature is that there is a sequence of stages, in each of which there is a major set of input axons that connect via a form of matrix with the output neurons of that stage. The type of computation that could be performed by one of these stages is considered first.

The perforant path connections with the dentate granule cells may be taken as an example. A version of this represented as a simplified matrix is shown in Fig. 2. Although the perforant path makes one set of synapses with the output neurons in a form of matrix, the matrix is clearly very different from an association matrix memory, in that in the hippocampal system there is no unconditioned stimulus that forces the output neurons to fire (see Rolls, 1987). Nor is there for each output cell a climbing fiber that acts as a teacher as in the cerebellum (see Ito, 1984; see Chapters 9 and 10 in this volume). In the hippocampal circuit there is apparently no teacher—that is, this appears to be an example of an unsupervised learning system. The following describes one mode of operation for such a network. Later, properties of the hippocampus that

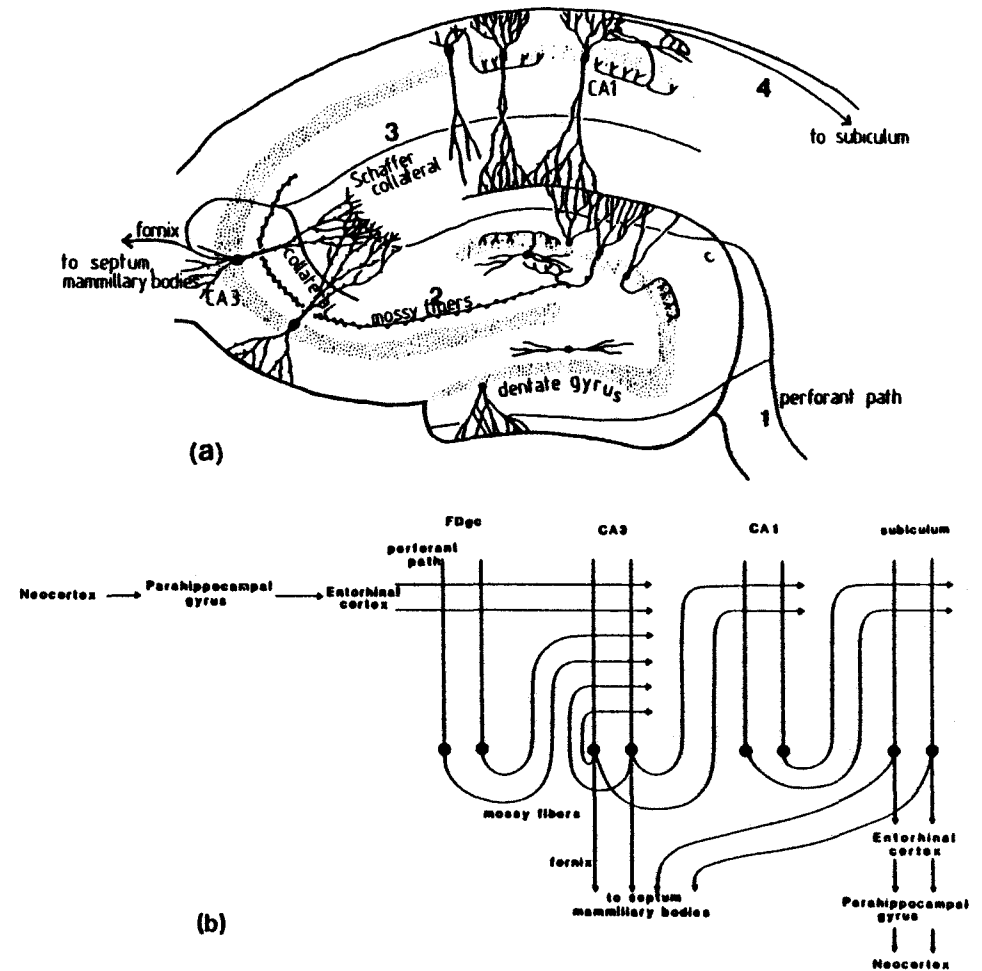


Figure 1.

(a) Representation of connections within the hippocampus. Inputs reach the hippocampus through the perforant path (1), which makes synapses with the dendrites of the dentate granule cells and also with the apical dendrites of the CA3 pyramidal cells. The dentate granule cells project via the mossy fibers (2) to the CA3 pyramidal cells. The well-developed recurrent collateral system of the CA3 cells is indicated. The CA3 pyramidal cells project via the Schaffer collaterals (3) to the CA1 pyramidal cells, which in turn have connections (4) to the subiculum. (b) Schematic representation of the connections of the hippocampus, showing also that the cerebral cortex (neocortex) is connected to the hippocampus via the parahippocampal gyrus and entorhinal cortex, and that the hippocampus projects back to the neocortex via the subiculum, entorhinal cortex, and parahippocampal gyrus.

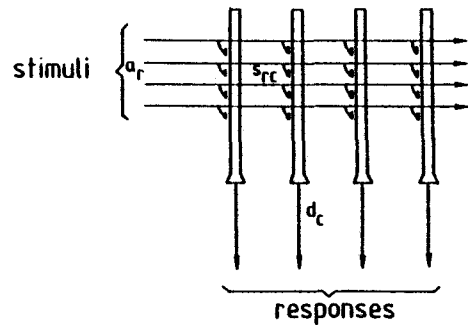


Figure 2.

A matrix for competitive learning in which the input stimuli are presented along the rows of the input axons (a_r), which make modifiable synapses (s_{rc}) with the dendrites of the output neurons, which form the columns (d_c) of the matrix.

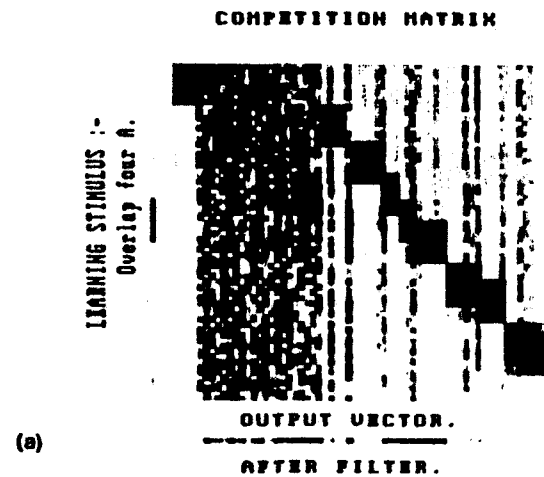
Consider a matrix memory of the form shown in Fig. 2 in which the strengths of the synapses between horizontal axons and the vertical dendrites are initially random (*postulate 1*). Because of these random initial synaptic weights, different input patterns on the horizontal axons will tend to activate different output neurons (in this case, granule cells). The tendency for each pattern to select or activate different neurons can then be enhanced by providing mutual inhibition between the output neurons, to prevent too many neurons responding to that stimulus (*postulate 2*). This competitive interaction can be viewed as enhancing the differences in the firing rates of the output cells [cf. the contrast enhancement described by Grossberg (1982)]. Synaptic modification then occurs according to the rules of long-term potentiation in the hippocampus, namely, that synapses between active afferent axons and strongly activated postsynaptic neurons increase in strength (see McNaughton, 1983; Levy, 1985; Kelso *et al.*, 1986; Wigstrom *et al.*, 1986; see Chapter 14 of this volume) (*postulate 3*). The effect of this modification is that the next time the same stimulus is repeated, the neuron responds more (because of the strengthened synapses), more inhibition of other neurons occurs, and then further modification to produce even greater selectivity is produced. The response of the system thus climbs over repeated iterations. One effect of this observed in simulations is that a few neurons then obtain such strong synaptic weights that almost any stimulus that has any input to that neuron will succeed in activating it. The solution to this is to limit the total synaptic weight that each output (postsynaptic) neuron can receive. In simulations this is performed by normalizing the sum of the synaptic weights on each neuron to a constant (e.g., 1.0) (cf. von der Malsburg, 1973; Rumelhart and Zipser, 1986). This has the effect

A simulation of the operation of such a matrix is shown in Fig. 3. It is shown that the network effectively selects different output neurons to respond to different combinations of active input horizontal lines. It thus performs a type of classification in which different complex input patterns are encoded economically onto a few output lines. It should be noted that this classification finds natural clusters in the input events; orthogonalizes the classes in that overlap in input events can become coded onto output neurons with less overlap, and in that many active input lines may be coded onto few active output lines; and does not allocate neurons to events that never occur (cf. Marr, 1970, 1971; Rumelhart and Zipser, 1986; Grossberg, 1982). It may be noted that there is no special correspondence between the input pattern and which output lines are selected. It is thus not useful for any associative mapping between an input and an output event, and is thus different from linear associative matrix memories (Rolls, 1987). Instead, this type of matrix finds associations or correlations between input events (which are expressed as sets of simultaneously active horizontal input lines or axons), allocates output neurons to reflect the complex event, and stores the required association between the input lines onto the few output neurons activated by each complex input event.

There is some evidence that in the hippocampus the synapses between inactive axons and active output neurons become weaker (see McNaughton, 1983; Levy, 1985). The effect of this in the learning system described would be to facilitate accurate and rapid classification, in that weakening synapses onto a postsynaptic neuron from axons that are not active when it is strongly activated would reduce the probability that it will respond to a stimulus that must be placed into a different class. It is also of interest that (*postulate 4*) it is not physiologically unreasonable that the total synaptic strength onto a postsynaptic neuron is somewhat fixed (Levy and Desmond, 1985).

Another feature of hippocampal circuitry is the mossy-fiber system, which connects the granule cells of the dentate gyrus to the CA3 pyramidal cells of the hippocampus. Each mossy fiber forms approximately 10 "mosses," in which there are dendrites of perhaps five different CA3 pyramidal cells. Thus each dentate granule cell may contact approximately 50 CA3 pyramidal cells (in the mouse; see Braitenberg and Schuz, 1983). In the rat, each mossy fiber forms approximately 14 "mosses" or contacts with CA3 cells, there are 1×10^6 dentate granule cells and thus 14×10^6 mosses onto 0.18×10^6 CA3 cells (D. Amaral, personal communication), and thus each CA3 pyramidal cell may be contacted by approximately 78 dentate granule cells. This means that (in the rat) the probability that a CA3 cell is contacted by a given dentate granule cell is $78 \text{ synapses}/10^6 \text{ granule cells} = 0.000078$. These mossy-fiber synapses are very large, presumably because with such a relatively small number

INPUT: { CYCLE: 202



INPUT: | CYCLE: 202

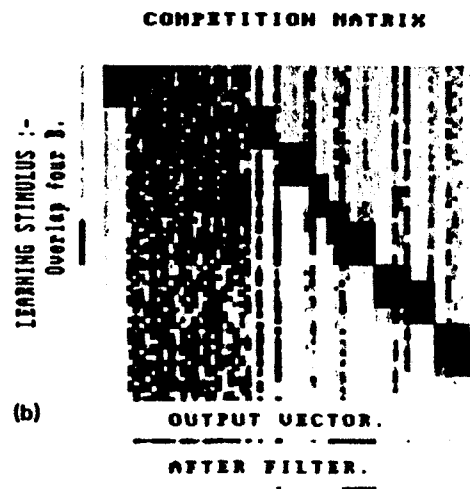


Figure 3.

Simulation of learning in a competitive matrix memory. The architecture is as shown in Fig. 2, except that there are 64 horizontal axons and 64 vertical dendrites, which form the row and columns, respectively, of the 64×64 matrix of synapses. The strength of each synapse, which was initially random, is indicated by the darkness of each pixel. The activity of each of the 64 input axons is represented in the 64-element vector at the left of the diagram by the darkness of each pixel. The output firing of the

One effect that can be achieved by this low probability of contact of a particular dentate granule cell with a particular pyramidal cell is pattern separation. This is achieved in the following way. Consider a pattern of firing present over a set of dentate granule cells. The probability that any two CA3 pyramidal cells receive synapses from a similar subset of the dentate granule cells is very low (because of the low probability of contact of any one dentate granule cell with a pyramidal cell), so that each CA3 pyramidal cell is influenced by a very different subset of the active dentate granule cells. Thus each pyramidal cell effectively samples a very small subset of the active granule cells, and it is therefore likely that each CA3 pyramidal cell will respond differently to the others, so that in this way pattern separation is achieved. [The effect is similar to codon formation described in other contexts by Marr (1970).] With modifiability of the mossy-fiber synapses, CA3 neurons learn to respond to just those subsets of activity that do occur in dentate granule cells. Moreover, because of the low probability of contact, and because of the competition between the CA3 neurons, the patterns that occur are evenly distributed over different ensembles of CA3 neurons. This pattern separation effect can be seen in Fig. 4. (It may be noted that even if competition does not operate in this system to increase orthogonality, then the low probability of connections just described would nevertheless mean that the hippocampus could operate to produce relatively orthogonal representations.)

It is notable that in addition to the mossy fiber inputs, the CA3 pyramidal cells also receive inputs directly from perforant path fibers

vertical neurons is represented in the same way by the output vectors at the bottom of the diagram. The upper output vector is the result of multiplying the input stimulus through the matrix of synaptic weights. The vector resulting from the application of competition between the output neurons (which produces contrast enhancement between the elements or neurons of the vector) is shown below by the vector labeled "after filter." The state of the matrix is shown after 203 cycles, in each of which stimuli with 8 of 64 active axons was presented and the matrix allowed to learn as described in the text. The stimuli were presented in random sequence, and consisted of a set of vectors that overlapped in 0, 1, 2, 3, 4, 5, or 6 positions with the next vector in the set. The columns of the matrix were sorted after the learning to bring similar columns together, so that the types of neuron formed, and the pattern of synapses formed on their dendrites, can be seen easily. The dendrites with random patterns of synapses have not been allocated to any of the input stimuli. It is shown that application of one of the input stimuli (overlap four A) produced one pattern of firing of the output neurons, and that application of input stimulus overlap four B produced a different pattern of firing of the output neurons. Thus the stimuli were correctly classified by the

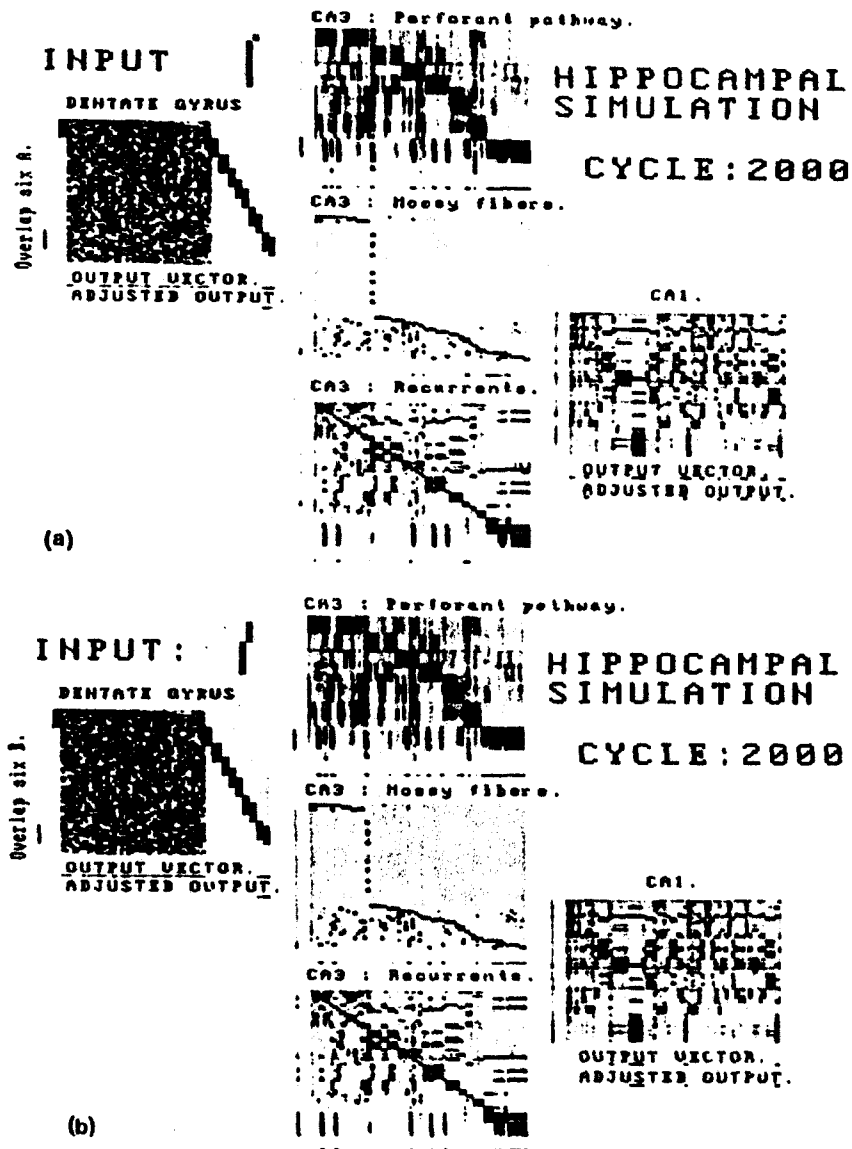


Figure 4.

Hippocampal stimulation. Conventions as in Fig. 3. The dentate gyrus is shown as a competition matrix at the left, receiving input stimuli from the perforant path. The vertical dendrites of the CA3 pyramidal cells extend throughout the three submatrices shown in the middle. The middle submatrix receives the output of the dentate granule cells via the mossy fibers with potentially powerful synapses and a low contact probability, and operates as a competition matrix. Pattern separation can be seen to operate in that input vectors are converted into output vectors with many

(see Figs. 1 and 2). This is not a sparse projection, in that each pyramidal cell may receive on the order of 2300 such synapses. [This is calculated using the evidence that of 15 mm of total dendritic length with 10,000 spines, approximately 3.5 mm (range 2.5–4.5 mm) is in the lacunosum moleculare and thus receives inputs from the perforant path (D. G. Amaral, personal communication).] What would be the effect of this input together with the very sparse, but strong, synapses from the mossy fibers? One effect is that the mossy-fiber input would cause the pattern of synapses (considered as a vector) on each pyramidal cell to point in a different direction in a multidimensional space. However, the precise direction in that multidimensional space could not be well specified by the relatively small number of mossy-fiber synapses onto each CA3 pyramidal cell. However, once pointed to that part of space by the mossy fibers, a particular cell would show cooperative Hebbian learning between its activation by the mossy input and the direct perforant path input, allowing the direct input to come by learning to specify the exact direction of that cell in multidimensional space much more effectively than by the coarse mossy-fiber input alone. This effect can be seen in Fig. 4. The relative weighting in this simulation was that the mossy-fiber input had an effect on each neuron that was five times greater than that of the direct perforant path input. Thus it is suggested that the combination of the sparse mossy-fiber input and the direct perforant path input is to achieve pattern separation, and at the same time to allow the response of the neuron to be determined not just by the sparse mossy-fiber input, but much more finely by making use in addition of the direct perforant path input.

An additional feature of the hippocampus, which is developed in the CA3 pyramidal cells in particular, is the presence of strong recurrent collaterals, which return from the output of the matrix to cross over the neurons of the matrix, as shown in Figs. 1 and 2. This anatomy immediately suggests that this is an autoassociation matrix. The effect of such recurrent collaterals is to make that part of the matrix into an autoassociation (or autocorrelation) matrix. The autoassociation arises because the output of the matrix, expressed as the firing rate of the CA3

and in that different output vectors are produced for even quite similar input vectors. The upper CA3 submatrix operates as a competition matrix with a direct perforant path input. The lower CA3 submatrix operates as an autoassociation matrix (formed by the recurrent collaterals). The output of the CA3 cells (summed vertically up and down the dendrite) is then used as the input (via the Schaffer collaterals) to the CA1 cells, which operate as a competition matrix. The states of the matrices after 2000 presentations of the same set of stimuli used for Fig. 3 are shown. One point demonstrated is that two very similar stimuli, overlap six A in Fig. 4a, and overlap six B in Fig. 4b, produce output vectors at CA1 that are

pyramidal cells, is fed back along the horizontally running axons so that the pattern of activity in this part of the matrix (the CA3 pyramidal cells) is associated with itself (see, e.g., Kohonen *et al.*, 1981; Rolls, 1987a). It can be noted here that for this suggestion to be the case, the synapses of the recurrent collaterals would have to be modifiable, and the modification rule would require alteration of synaptic strength when both the presynaptic fiber and the postsynaptic dendrite were strongly activated. Further, the probability of contact of the neurons in the autoassociation matrix must not be very low if it is to operate usefully (see Marr, 1971). Given that the region of the CA3 cell dendrites on which the recurrent collaterals synapse is long (approximately 11.5 mm), and that the total dendritic length is approximately 15 mm and has approximately 10,000 spines (D. G. Amaral, personal communication), approximately 7700 synapses per CA3 pyramidal cell could be devoted to recurrent collaterals, which with 180,000 CA3 neurons in the rat makes the probability of contact between the CA3 neurons 0.043. This is high enough for the system to operate usefully as an autoassociation memory (see Marr, 1971). It is remarkable that the contact probability is so high, and also that the CA3 recurrent collateral axons travel so widely in all directions that they can potentially come close to almost all other CA3 neurons (D. G. Amaral, personal communication).

The importance of the autoassociation performed by this part of the matrix is that it forms a recognition memory, with all the advantageous emergent properties of a matrix memory, such as completion, generalization, and graceful degradation (see Kohonen *et al.*, 1977, 1981; Kohonen, 1984; Rolls, 1987). One property that is particularly relevant here is completion, in that if part of a stimulus (or event) occurs, then the autoassociation part of the matrix completes that event. Completion may operate particularly effectively here, because it operates after the granule-cell stage, which will reduce the proportion of neurons firing to represent an input event to a low number partly because of the low probability of contact of the granule cells with the CA3 pyramidal cells. It is under these conditions that the simple autocorrelation effect can reconstruct the whole of one pattern without interference, which would arise if too high a proportion of the input neurons was active. It is of interest that a scheme of this type, although expressed in a different way to the autoassociation matrix formulation, was proposed by Marr in 1971. Another effect of the autoassociation matrix is that patterns of activity that are not similar to those already learned by this type of recognition memory are lost, so that noisy patterns can be cleaned up by the autoassociation matrix. It is further notable that these completion and cleaning-up processes benefit from several iterations (repeated cycles) of the autoassociation feedback effect. It has been suggested by B. McNaughton (personal communication, 1987) that one function of hippocampal theta activity may be to allow this autoassociative effect to be

duced by the recurrent collaterals to cycle for several iterations (in a period of approximately 50 msec), and then to stop, so that the system can operate again with maximal sensitivity to new inputs received on the mossy fiber and perforant path systems by the CA3 cells.

The CA1 pyramidal cells that receive from the CA3 cells are considered to form a further stage of competitive learning, which has the effect of further classification of signals received, perhaps enabled by the pattern of connections within the hippocampus to form these classifications over inputs received from any part of the association neocortex. The firing of the CA1 cells would thus achieve a much more economical and orthogonal classification of signals than that present in the perforant path input to the hippocampus. These signals are then returned to the association neocortex via the subiculum, entorhinal cortex, and parahippocampal gyrus, as indicated in Figs. 1 and 2. It is suggested below that one role that these economical (in terms of the number of activated fibers) and relatively orthogonal signals play in neocortical function is to guide information storage or consolidation in the neocortex.

It may be noted that multilayer networks (such as the hippocampus) can potentially solve classes of problems that cannot be solved in principle by single-layer nets (Rumelhart and Zipser, 1986). This is because subcategories formed in an early stage of processing can enable a later stage to find solutions or categories that are not linearly separable in the input information space.

Having considered the computational theory of how the hippocampal circuitry may function, we can now turn to a systems-level analysis, in which the inputs and outputs of the hippocampus are considered, and the function performed by the hippocampus in relation to overall brain function can be formulated.

III. Systems-Level Theory of Hippocampal Function

First the anatomical connections of the primate hippocampus with the rest of the brain will be considered, in order to provide a basis for considering how the computational ability of the hippocampus could be used by the rest of the brain.

The hippocampus receives inputs by two main routes, the entorhinal cortex and the fimbria/fornix. The entorhinal cortex (area 28) provides it with extensive inputs from the neocortex (see Fig. 5). Thus all temporal neocortical areas project to area 35, the perirhinal cortex, or to area TF-TH, in the parahippocampal gyrus, which in turn projects to the entorhinal cortex (Van Hoesen and Pandya, 1975a,b; Van Hoesen, 1982; Amaral, 1987). The parietal cortex (area 7) projects to area TF-TH

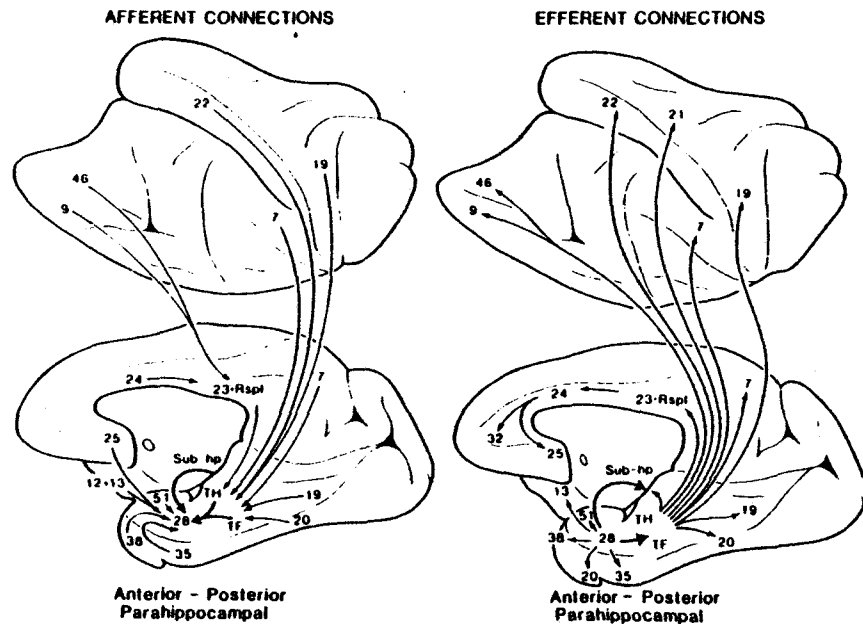


Figure 5.

Connections of the primate hippocampus with the neocortex (from Van Hoesen, 1982). A medial view of the macaque brain is shown below, and a lateral view is shown inverted above. The hippocampus receives its inputs via the parahippocampal gyrus, areas TF and TH, and the entorhinal cortex, area 28. The return projections to the neocortex (shown on the right) pass through the same areas. Cortical areas 19, 20, and 21 are visual association areas, 22 is auditory association cortex, 7 is parietal association cortex, and 9, 46, 12, and 13 are frontal cortical association areas.

cortex, areas 12 and 13, projects directly to the entorhinal cortex (Van Hoesen *et al.*, 1975). In addition, the entorhinal cortex receives inputs from the amygdala. The entorhinal cortex itself projects via the perforant path to reach primarily the dentate granule cells of the hippocampus proper. Thus by these routes the hippocampus receives information after it has been highly processed through the temporal, parietal, and frontal cortices. It must thus be of great importance for hippocampal function in the primate that by its main input, the perforant path, it receives information from the highest parts of the neocortex. There are also inputs to the hippocampus via the fimbria/fornix from the cholinergic cells of the medial septum and the adjoining limb of the diagonal band of Broca. The hippocampus also receives a noradrenergic input from the locus coeruleus, and a 5-hydroxytryptamine (5-HT) input from the median raphe nucleus.

A major output of the hippocampus arises from the hippocampal pyramidal cells, and projects back via the subiculum to the entorhinal

cortex, which in turn has connections back to area TF-TH, which in turn projects back to the neocortical areas from which it receives inputs (Van Hoesen, 1982) (see Figs. 5 and 1). Thus the hippocampus can potentially influence the neocortical regions from which it receives inputs. This is the pathway suggested as being involved in guiding memory storage in the neocortex. A second efferent projection of the hippocampal system reaches the subiculum from the CA1 pyramidal cells, and travels via the fimbria and (postcommissural) fornix to the anterior thalamus, and to the mammillary bodies, which in turn project to the anterior thalamus. The anterior thalamus in turn projects into the cingulate cortex, which itself has connections to the supplementary motor cortex, providing a potential route for the hippocampus to influence motor output (Van Hoesen, 1982). It is suggested that functions of the hippocampus in, for example, conditional spatial response learning utilize this output path to the motor system.

The connections of the hippocampus with other parts of the brain, and the internal connections and synaptic modifiability described above, suggest that the hippocampus should be able to detect, and classify onto a few specifically responding neurons, specific conjunctions of complex (cortically processed) events, such as that a particular object (presumably reflecting temporal lobe visual processing) has appeared in a particular position in space (presumably reflecting parietal input). Another example might be that a particular stimulus should be associated with a particular spatial motor response. It has been shown above that this is the type of quite specific information that comes to activate different hippocampal neurons while monkeys are performing object-place memory and conditional spatial response learning tasks. Indeed, the neurophysiological findings described above provide evidence that supports the model of hippocampal function just described. The model is also supported by the evidence that during learning of conditional spatial responses some hippocampal neurons start, but then stop, showing differential responses to the different stimuli, consistent with competitive interactions between hippocampal neurons during learning, so that only some hippocampal neurons become allocated to any one learned event or contingency (see above).

The analyses above have shown that the hippocampus receives from high-order areas of association cortex; is able by virtue of the large number of synapses on its dendrites to detect conjunctions of events even when these are widely separated in information space, with their origin from quite different cortical areas; allocates neurons to code efficiently for these conjunctions probably using a competitive learning mechanism; and has connections back to the neocortical areas from which it receives, as well as to subcortical structures via the fimbria/fornix system. What could be achieved by this system? It appears that the long-