Attractor Neural Network Models of Spatial Maps in Hippocampus

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ABSTRACT: Hippocampal pyramidal neurons in rats are selectively activated at specific locations in an environment (O'Keefe and Dostrovsky, Brain Res 1971;34:171-175). Different cells are active in different places, therefore providing a faithful representation of the environment in which every spatial location is mapped to a particular population state of activity of place cells (Wilson and McNaughton, Science 1993;261:1055-1058; Zhang et al., J Neurosci 1998;18:1017-1044). We describe a theory of the hippocampus, according to which the map results from the cooperative dynamics of network, in which the strength of synaptic interaction between the neurons depends on the distance between their place fields. This synaptic structure guarantees that the network possesses a quasi-continuous set of stable states (attractors) that are localized in the space of neuronal variables reflecting their synaptic interactions, rather than their physical location in the hippocampus. As a consequence of the stable states, the network can exhibit place selective activity even without relying on input from external sensory cues. Hippocampus 1999;9:481-489. © 1999 Wiley-Liss, Inc.

Pyramidal place cells of the rat's hippocampus often fire in particular regions of an apparatus (O'Keefe and Dostrovsky, 1971). Recently, it has become possible to record from over one hundred hippocampal neurons simultaneously. There is sufficient information in these cells to encode the position of the animal in its environment, which suggests that place cells are involved with some aspects of navigation (Wilson and McNaughton, 1993; Zhang et al., 1998). Although the activity of place cells in a familiar environment can be controlled by constellations of various landmarks (O'Keefe and Speakman, 1987; Tanila et al., 1997), it is not simply a direct reflection of sensory inputs as was assumed in earlier theories (Zipser, 1985; Sharp, 1991). A place cell can continue firing when the rat is in the appropriate location for some time after the removal of visual cues, or switching off the lights (O'Keefe and Speakman, 1987; McNaughton et al., 1989; Quirk et al., 1990; Mark and Maks, 1994). Furthermore, the positions of place fields in a given environment can also be modified by changing the behavior of the rat (Mark and Maks, 1995). Therefore, these neurons represent a more abstract set of relationships between sensory cues and the past history of the rat in a particular environment. Several recent models have tried to explain these striking properties by considering the activity of hippocampal networks during spatial locomotion as a special type of attractor dynamics. The Attractor Neural Network (ANN) theory was originally introduced in relation with associative memory (see Amit, 1989) and subsequently proposed as a model of the CA3 region of the hippocampus (Rolls, 1989) in view of this region's high degree of connectivity and the hippocampus's alleged involvement in episodic memory (Scoville and Milner, 1957; Squire et al., 1989). Applying it to the problem of place cells and spatial navigation may, therefore, be an attractive unifying view of the hippocampus and could serve to substantiate the idea of hippocampus as a cognitive map (O'Keefe and Nadel, 1978).

How can one apply the theory of ANNs to the place coding in the hippocampus? In a typical ANN, the memories are realized as a discrete set of stable activity states (called attractors) of the network, "learned" by appropriate modification of the connections strengths between participating neurons, with high-energy barriers between the attractors (Hopfield, 1982). Any initial state of the network that is sufficiently similar to one of the memory states will subsequently converge to the corresponding attractor by virtue of the intrinsic network dynamics. In such a system, smooth transitions between attractors are impossible, which makes it unsuitable as a model of continuous change in the activity of hippocampal neuronal populations while the animal explores the environment. One, therefore, has to adapt the original ANN model to allow the attractor states to form a continuous set with little or no barriers between the neighboring states. Similar adaptation was earlier performed in network models of population vector coding in motor cortex (Lukashin and Georgopoulos, 1993) and orientation selectivity in primary visual cortex (Ben-Yishai et al., 1995) and can with certain modifications be applied to spatial maps (Tsodyks and Sejnowski, 1995a; McNaughton et al., 1996; Samsonovich and McNaughton, 1997; Redish and Touretzky, 1998). The crucial assumption for this model is that the strength of connection between place cells should be a decremental function of the distance between their place fields, which was earlier proposed in Muller et al. (1991b).

If, indeed, the hippocampus is an ANN with a continuous set of attractors, this would explain how a coherent representation of a particular location could be stable in the absence of external cues. However, this representation has to be constantly updated while the animal moves around the environment. It was proposed that this task is accomplished by the combination of external cues (if they are present) and internal feedback.
generated by integration of the animal's movements (path integration) (O'Keefe, 1976; Muller et al., 1991a; McNaughton et al., 1996; Taube et al., 1990; Mizumori and Williams, 1993; Chen et al., 1994). One way the path integration system could work in interaction with an attractor representation of spatial location was proposed in Samsonovich and McNaughton (1997).

A further issue arises if one considers hippocampal spatial maps of different environments. The spatial location of place fields upon subsequent reintroductions of the animal into the same environment was shown to be reproducible even if done intermittently with exploring other environments (Barnes et al., 1997). Surprisingly, however, comparing the activity of populations of place cells in different environments revealed no apparent similarity between the relative positions of place fields (Bostok et al., 1991; Markus et al., 1994). The hippocampus is, therefore, capable of permanently keeping many uncorrelated spatial maps. Correspondingly, the attractor model would require storing many sets of continuous attractors (called “charts” in McNaughton et al., 1996; see also Kube and Muller, 1991; Muller et al., 1996) in the same network. Although this property may appear analogous to the ability of the Hopfield network to store numerous memories, one has to keep in mind that each chart by itself represents a (quasi) continuous set of attractors, which raises the question of how many charts can in principle be stored in one network. This problem was analyzed quantitatively in Battaglia (1998).

Finally, the firing patterns of pyramidal cells in the CA1 and CA3 regions of the rat hippocampus are related to both the location of the animal in the environment and the theta rhythm, which dominates the hippocampal EEG during exploratory movements (Vanderwolf, 1969). O'Keefe and Recce (1993) have observed that at each location within the place field of a cell, there is a tendency for the cell to fire preferentially at a particular phase of the theta rhythm, and the preferred phase of firing advances as the rat passes through the field (see also Skaggs et al., 1996). Thus, the precise timing of the cell's firing relative to the theta rhythm provides information about whether the rat is moving into or out of the cell's place field. This observation may have interesting implications for the general problem of temporal coding in spike trains (Richmond and Optican, 1990; Blaek et al., 1991; Tovee et al., 1993). The neuronal mechanisms underlying this phase precession effect are still unknown. Viewed as a network property, progression of phases indicates the presence of a fast wave of activity progressing in the direction corresponding to the direction of the animal's movement, which starts at the beginning of each theta cycle and subsides at the cycles end (Tsodyks et al., 1996; Wallenstein and Hasselmo, 1997). This wave can come about in the ANN network if one assumes that connections between place cells are stronger in the direction corresponding to the current direction of animals' movement.

In the following sections, the attractor network model of the hippocampus is presented in more detail. I then discuss the possible anatomical and physiological correlates of the most important aspects of the network and review the experimental evidence in favor of and against the model.

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**ANN MODEL OF THE HIPPOCAMPAL NETWORK**

Here I illustrate the idea of hippocampus as an attractor network in the simplest situation in which the animal runs through a linear track in one direction only (Tsodyks and Sejnowski, 1995a). The network can be modeled by a set of neurons labeled by the positions of their place fields, xi, as would be determined by extra-hippocampal input; that is, the location in the environment where the cell is most strongly activated by this input. The model is based on the mean-field approximation in which the average firing rates of the neurons enter into the model (Wilson and Cowan, 1972; Grossberg, 1988):

\[
\frac{d r_i}{dt} = -r_i + g(S_i J_{ij} r_j + I_i),
\]

where \( r_i \) is the average spiking rate of the neuron \( i \), \( I_i \) is its external sensory input, \( g(x) \) is the gain function of the neurons, \( J_{ij} \) is the strength of the synaptic coupling between the neurons \( i \) and \( j \) with the labels \( x_i \) and \( x_j \), respectively. The gain function \( g \) can be chosen in a semi-linear form with threshold: \( g(h) = \beta(h - T) \) for \( h > T \) and 0 otherwise.

The crucial assumption of the model pertains to the structure of the synaptic connections. To make the network possess a continuous set of stable attractor states, each corresponding to different locations on the track, the strength of the connection between the cells has to be a decremental function of the distance between their fields (see also Lukashin and Georgopoulos, 1993; Ben-Yishai et al., 1995; Muller et al., 1991b). The exact form of this function is not important, so one can assume a simple exponential dependence:

\[
J_{ij} = F (x_i - x_j) = J_0 \exp(-|x_i - x_j|/\sigma) - J_1.
\]

The uniform inhibitory term \( J_1 \) can be considered a global feedback inhibition mediated by interneurons, which insures a competition between pyramidal cells. Notice that Eq. 2 implies that the strength of connection between a pair of neurons is symmetric. However, as was elaborated in the standard theory of associative memory networks, introduction of random asymmetry by, e.g., randomly diluting the connections, does not modify the stable states of the network (Amit, 1989).

The extra-hippocampal excitatory input \( I \) should provide the hippocampus with information about the position of the animal on the track. Again, an exponential dependence can be assumed:

\[
I_i = I_0(1 + \lambda \exp(-|x_i - x_0|/\xi)),
\]

where \( x_0 \) is the current position of the animal on the track. Thus, the cell receives maximal input when the rat is in the center of its place field: \( x_i = x_0 \). For the moment, we ignore the possibility that...
part of the extra-hippocampal input may include the contribution of the path-integration system. The place specificity of the extra-hippocampal input is described by two parameters: \( \lambda \), the strength of modulation, and \( I \), the width of tuning. Consider first an ideal case where the initial place fields \( x_i \) are positioned equidistantly over the length of the track.

If there are no external cues in the environment, the place-specific modulation of the input is zero, i.e., \( \lambda = 0 \). However, even in this case the activity state of the network is not uniform if the connections between the neurons are strong enough (Ben-Yishai et al., 1995). Instead, due to a combination of excitation between cells with neighboring fields and global inhibition, the network converges to one of the set of stable attractor states, all with the same shape, centered around each position \( x_i \). An example of such an attractor is shown in Figure 1. Since there are no barriers between nearby attractors, each of them is only marginally stable. The particular state of activation, therefore, depends entirely on the initial activation pattern. If cues are present, the external input has a nonzero modulation and the actual position of peak activation would be determined by the peak of the input; that is, by the position of the animal \( x_o \). This model can easily be extended to a two-dimensional, open-field environment, in which case each neuron is labeled by a two-dimensional vector \( r \), corresponding to the location of its place field (McnAughton et al., 1996; Samsonovich and McnAughton, 1997; Redish and Touretzky, 1998).

While the animal moves through the environment, the peak of the input moves accordingly through the network, causing the activity to shift continuously from one attractor to another. As a consequence, subsequent neurons in the network will have uniformly distributed place fields along the duration of the track, with possible distortions at the beginning and the end of the track. In the absence of external cues, the driving force for such an activity wave through the set of attractor states has to come from the path integration system. To imagine how this could come about, one can note that such a wave is generated in the network if an antisymmetric component is added to the connections between the neurons, such that for each pair of neurons the connection is stronger in the direction of the wave. This idea was previously applied by Lukashin and Georgopoulos (1993) to model the so-called “mental rotation” of the population vector. The speed of the wave is proportional to the strength of the asymmetry in the connections and, therefore, has to be determined by the velocity of the animal so that the transitions between the neighboring attractors would proceed with the appropriate speed. We postpone consideration of the possible neuronal mechanisms that could be responsible for generating this effective asymmetry of connections until the Discussion.

**FIGURE 1.** Firing rate (in fraction of the saturating rate) of all of the neurons in the network at one of the stable states. Each neuron is labeled by its corresponding \( x_i \) normalized by the length of the track.

\[
J_j = \sum_{n=1}^{N} F(r^+_n - r^+_j),
\]

where the function \( F \) has the same form as in Eq. 2. Here \( r^+_n \) refers to the (two-dimensional) label of the neuron in the chart number \( n \), which becomes associated with the center of the place field of this neuron in the environment where this chart is activated; \( N \) is the overall number of charts. According to the reasoning given above, one can assume that individual charts are close to being uncorrelated, i.e., there is no structural similarity in the relative distances between the neuron’s place fields in different environments. This means that if the network dynamics converges to an attractor state corresponding to a certain location in one of the environments (e.g., due to the appropriate external input), this state looks completely random in the coordinates corresponding to the labeling of cells in another chart (Fig. 2).

While the network converges to one of the attractors in one of the charts, the input to each neuron, coming from the term in the connection matrix of Eq. 4 that corresponds to the “active” chart, act in concert to stabilize the attractor state. However, the contributions coming from the other charts act as random, noisy input. The question, therefore, arises as to whether the network can support many charts before the interference between them makes the attractor states unstable. This issue was analyzed in detail in Battaglia (1998). The result of the analysis can be
the firing of place cells is modulated by the theta rhythm in such a way that at each location within the place field, the cell tends to fire at a particular phase of the rhythm. Moreover, the preferred phase of firing advances steadily as the rat passes through the field, therefore providing additional information about the animal’s location within the field.

The origin of the phase precession could lie in the interaction between septal and cortical inputs to the hippocampus (O’Keeffe and Recce, 1993; Burgess et al., 1994), which would require special assumptions about the temporal relations between these two inputs. Here I describe the possibility that the phase precession effect results from the intrinsic activity dynamics in the hippocampus in the framework of the ANN model (Tsodyks et al., 1996; Wallenstein and Hasselmo, 1997). Viewed as a network property, the phase precession effect indicates that at each theta cycle the network generates a fast wave of activity propagating along the subset of cells whose place fields lie in the order corresponding to the direction of the animal’s motion (see Fig. 3).

This could be accomplished if one assumes that the connections between neurons with neighboring place fields are asymmetric, being stronger in the direction corresponding to the animal’s movement. The wave starts at the phase of theta where the population activity is on the rise and terminates at the phase where it subsides below a certain critical level. Which neuron gives rise to a wave depends on the current position of the animal, so at each subsequent cycle the wave starts from neurons with slightly displaced place fields in accordance with the animal’s velocity. In the model, the wave starts with the neuron that at the moment receives the strongest extra-hippocampal input (see Eq. 3).

This model reproduces most of the properties of phase precession observed experimentally. In particular, since the asymmetry of connections is assumed here to be fixed (independent of the animal’s speed), the speed of the activity wave does not depend on the speed of the animal. Thus the phase of theta at which a neuron fires, which depends on the time it takes for the wave to reach the neuron, is determined by the current location of the animal within the neuron’s place field and not on the time passed since entering the field, in agreement with experimental evidence (O’Keeffe and Recce, 1993). Note that in contrast to what was said in relation to path integration mechanisms, the wave in Figure 3 has to be faster than what is required to account for the velocity of the animal. Both asymmetry of connections and place-specific external input are, therefore, needed to reproduce the phase precession effect.

**DISCUSSION**

The ANN theory of the hippocampus has the ability to explain in a unifying way some of the most striking properties of place cells, which are hard to account for by other models. The anatomical and physiological realization of some of the ingredients of ANN networks described in the previous section was
intentionally left ambiguous, which in my view reflects the current level of experimental evidence. Here, I discuss various possibilities proposed in the literature together with some further experimental results. In the final analysis, only unambiguous formulations will make the model useful in deriving experimental predictions and eventually help to either prove or reject ANNs as a relevant model for spatial mapping in the hippocampus.

Origin of the Synaptic Matrix

What could be the origin of the synaptic matrix postulated in the model? One possible answer would be that synaptic connections between neurons with neighboring place fields are reinforced during exploration by some sort of Hebbian mechanism (see, e.g., Muller et al., 1996; Wallenstein and Hasselmo, 1997; Brunel and Trullier, 1998). In other words, during the first visit to the environment, the cells are mainly driven by external cues. If a pair of cells are driven in nearby locations, they will fire in temporal proximity, which will lead to potentiation of connections between them. If the animal moves along stereotyped trajectories, e.g., along a linear track, cells with neighboring fields would fire in a fixed temporal order, which could lead to asymmetrical strengthening of their connections (Levy and Steward, 1983; Markram et al., 1997). There is some indirect experimental evidence for synaptic plasticity during exploration. Wilson and M'cnaughton (1994) recorded a population of place cells in a sleep session immediately after exploration. Selective increased correlations in the activity in pairs of cells whose place fields were overlapping during the preceding behaving session were reported. Moreover, such pairs of cells exhibited a tendency to fire during sleep in the temporal order, reflecting the order in which their fields were passed by the animal (Skaggs and M'cnaughton, 1996). Another piece of evidence for asymmetric synaptic modification was the observation by M'eha et al. (1997) that on linear tracks, place fields tend to expand, over the course of each behavioral session, in

FIGURE 3. Spiking activity in a network model composed of integrate-and-fire neurons, during a simulated run of a rat through a linear apparatus. For each spike of an excitatory neuron \( i \), the position label \( x_i \) of the neuron is plotted on the vertical axis, against the time at which the spike was emitted (horizontal axis). Vertical lines mark the phase of the theta cycle at which the activity of the network is minimal. The shallow overall slope is determined by the velocity of the rat; the steep slope within each theta cycle is determined by the internal dynamics of the network.
the direction opposite to the direction of movement, which could result from such modifications as predicted theoretically (Blum and Abbott, 1995).

Although these observations are compatible with the idea of attractor states being learned during exploration, evidence against it also exists. Quirk et al. (1990) introduced rats in total darkness to a previously explored environment. In many cases, new place fields developed that then remained stable after re-introduction of light. Another piece of evidence can be found in instances of complete re-mapping of a familiar environment that were observed in old rats (Barnes et al., 1997). These and other observations motivated McNaughton et al. (1996) to formulate a hypothesis according to which the hippocampus contains an intrinsically stored set of two-dimensional maps, called charts, due to a pre-wired matrix of synaptic connections in the form of Eq. 4. Each time the animal enters a new environment, one of these representations is chosen, which then becomes associated with external cues during subsequent exploration. This associating could result from Hebbian potentiation of connections that project to the hippocampus from the neurons responding to sensory cues. Although compatible with the above-mentioned evidence, this interpretation is also not free of its problems. Since in this picture the selection of the map occurs right at the beginning of exploration, maps corresponding to different environments should be either identical or uncorrelated, independently of how similar these environments are. Recent observations showed, however, that when a rat explored two interconnected boxes of identical shape, the number of identical place fields in the boxes was significantly above chance, indicating that the corresponding maps were partially correlated (Skaggs and McNaughton, 1998). Similarly, Jeffrey et al. (unpublished data) studied the development of the spatial map in a box whose location relative to the outside cues was gradually shifted. In this study, too, partial re-mapping was observed. Tanila et al. (1997) rearranged visual cues in a familiar environment. This led to development of new place fields, which occurred on a time course of 5 to 30 min. Taken together, all the evidence collected up to now seems to indicate that sensory cues, if present, can to a large degree determine the nature of the resulting map in a given environment, possibly by causing additional synaptic modification between place cells on top of synaptic structure that is either pre-wired or acquired by previous experiences of the animal. This issue will have to be further explored in both theoretical and experimental studies.

What Drives the Place Cells

There is no consensus on where the major input carrying place-specific information comes from, and what the strength of the extra-hippocampal input to a neuron is, relative to the input coming from within the hippocampus from other pyramidal cells. In its extreme form, ANN theory assumes that the major input to a neuron originates from within the network, and the role of extra-hippocampal input is mainly reduced to determining the correct attractor in the given chart, and/or correct chart out of many stored. An interesting implication of the ANN hypothesis relates to a situation when the external input is in conflict with the current location of the attractor state. In this case, the activity profile gradually moves toward the input, going through all the intermediate locations instead of jumping to the new location directly (Ben-Yishai et al., 1995). Obviously, no such movement would be observed if the neurons are driven directly by extra-hippocampal input. This conflict was realized in Gothard et al. (1996), where a rat ran along a linear track, starting from a box located on one of the ends. After a period of training on this apparatus, the location of the box was shifted to a different point on the track while the rat was moving toward the other end of the track. Since some of the cells had fields inside the box, at the beginning of the out-of-box journey the input from the external cues was in conflict with the activation pattern of the network at that moment. For all of the new locations of the box, most of the place cells were active in the same temporal order as for the old location, indicating that the network was mainly undergoing a transition from the activity state within the box until it reached the location required by the external cues. This experiment provides strong support for the idea that the intrinsic dynamics of activity of hippocampal networks, and not external sensory cues, provides the major driving input to place cells firing.

Path Integration Mechanism and Activity of Place Cells

To keep track of current location based on self-motion, the path integration system has to utilize information about the direction and velocity of motion. In fact, directional cells have been found in several sub-cortical areas (Ranck, 1984; Taube et al., 1990; Mizumori and Williams, 1993; Chen et al., 1994). The working mechanisms and anatomical location of the path integration circuitry are not yet discovered. As previously discussed, it could include ANN as its component by inducing the asymmetry in the connections between place cells and, therefore, causing the activity to propagate along the subsequent attractor states. This could be done directly by facilitating synaptic transmission between place cells by axo-axonic input from motion-sensitive cells. An alternative arrangement was proposed in McNaughton et al. (1996), according to which the hippocampus interacts with a parallel network of neurons that receive inputs both from hippocampus and motion cells. Each motion cell projects back to the hippocampus with an offset bias corresponding to the preferred direction of the cell. This way, depending on the direction of motion, synaptic excitation between place cells, mediated by motion cells, will be selectively strengthened, effectively creating the required asymmetric component in the interactions.

Alternatively, the path integration circuitry could be separate from the hippocampus, e.g., in subiculum (Sharp et al., 1995) or parasubiculum (Redish and Touretzky, 1997). Redish and Touretzky (1997) propose that the path integration system receives a reset signal from the hippocampus each time the animal enters a familiar environment. Subsequently, it updates its representation of the current location relative to the starting point by constantly adding the velocity vector. This circuitry could then provide the
hippocampus (via superficial layers of entorhinal cortex) with an input reflecting the current location of the animal relative to the starting point, i.e., of a form similar to Eq. 3. Direction-dependent asymmetric strengthening of connections between place fields could still take place due to the input from head-direction cells, which would explain the phase precession effect.

Directionality of Place Cells

While an animal runs along a linear track, the majority of cells fire only in one of the two possible movement directions (Muller et al., 1994; Markus et al., 1995). However, most place cells (about 80%) are non-directional when the animal freely explores open environments. Moreover, the degree of the directionality depends on the pattern of exploration. When the animal switches from random exploration to moving along stereotyped trajectories, many cells become more directional (Markus et al., 1995). These still unexplained observations could have important implications for the attractor theory of place cells. If place fields are initially driven by external cues, one has to assume that the fields should first appear with at least some degree of directional specificity. During subsequent exploration in an open-field environment, when the animal is free to make random turns, fast Hebbian plasticity could develop connections between fields with various directions, thus leading to an omni-directional representation (Brunel and Trullier, 1998).

A very different explanation to this problem is given in the framework of pre-wired connections (McNaughton et al., 1996). According to this explanation, the place representation is intrinsically two-dimensional and is supported by a built-in set of uncorrelated charts. As the rat changes direction on the linear track, a sudden switch from one chart to another occurs, so that a different set of cells will be active for each direction. While this explanation is compatible with the data, the mechanism of switching between the charts is not specified.

Distribution of Place Fields

Here we focus on the possible experimental consequences of modification of the synaptic matrix during exploration. Tsodyks and Sejnowski (1995a) noted that since continuous attractors are only marginally stable, introduction of inhomogeneity in the distribution of synaptic coupling parameters, should lead to significant rearrangement in the layout of attractors. In particular, a continuous set of attractors collapsed to a smaller number of attractors, whose location is determined by groups of neurons with stronger interactions. As a result of this collapse, when the input traverses the network while the rat moves from one end of the apparatus to the other, the activity does not progress smoothly, but rather experiences a set of jumps with magnitudes depending on the relative strength of intra- and extra-hippocampal inputs. This is illustrated in Figure 4 where I plot the solutions of Eq. 1 for all possible locations of the animal on the linear track. One can see that there is considerable discontinuity in the activity as the input activity sweeps across the network.

As a result, the distribution of place fields in the apparatus, instead of being uniform, should exhibit some degree of clustering near the places where many individual attractors collapse together. Place fields corresponding to the same attractor should have similar size. The same conclusion was reached in more realistic simulations of two-dimensional environments with ongoing Hebbian modification of synaptic connections during exploration (Brunel and Trullier, 1998). In the model, the collapse of individual attractors into collective ones with large basins of attraction generally occurs in regions of increased strength of recurrent synapses. This inhomogeneity of recurrent synaptic couplings could result from varying conditions in the environment, such as bends in the maze where the rat must turn, locations of food, or other unique conditions. Experimental studies of place field distribution are sparse. Clustering of fields was observed by Eichenbaum et al. (1989) and O'Keefe and Recce (1993) but not...
The attractor model of place coding in the hippocampus provides a unifying explanation of many experimentally observed properties of place cells. The central hypothesis of the model is that the activity of place cells in the CA3 area of the hippocampus results from the interactive dynamics of an associative network of neurons. According to the model, cells with nearby place fields are not random, but rather organized in highly correlated two-dimensional charts, with different charts being largely uncorrelated with each other. They could however become correlated due to the experiences of the rat. The attractors are evoked by the combination of external sensory and internal motion signals originating from outside of the hippocampus. There are many open questions regarding the anatomical and physiological correlates of several crucial aspects of the model, such as the nature of the input and the origin of synaptic connections. To resolve these ambiguities and more directly confront the model with experimental observations, the interactions between the hippocampus and the other brain structures involved in navigation, such as the entorhinal cortex and subiculum (Sharp, 1997), need to be studied in more detail.

**REFERENCES**


Quirk GJ, Muller RU, Kubie JL. 1990. The firing of hippocampal place
cells in the dark depends on the rat's previous experience. J Neurosci

Ranck Jr, JB. 1984. Head direction cells in the deep cell layer of dorsal

Redish AD, Touretzky DS. 1997. Cognitive maps beyond the hippocam-

Redish AD, Touretzky DS. 1998. The role of the hippocampus in solving

Richmond BJ, Optican LM. 1990. Temporal encoding of two-
dimensional patterns by single units in primate primary visual cortex:

Rolls ET. 1989. Functions of neuronal networks in the hippocampus and
neocortex in memory. In: Byrne JH, Berry WO, editors. Neural

mapping in a continuous attractor neural network model. J Neurosci
17:5900–5920.

Scoville WB, Milner B. 1957. Loss of recent memory after bilateral


Sharp PE. 1997. Subicular cells generate similar spatial firing patterns in
two geometrically and visually distinctive environments: comparison

Sharp PE, Blair HT, Etkin D, Tzianos DB. 1995. Influences of vestibular
and visual motion information on the spatial firing patterns of

Skaggs WE, McNaughton BL. 1996. Replay of neuronal firing sequences
in rat hippocampus during sleep following spatial experience. Science
271:1870–1873.

Skaggs WE, McNaughton BL. 1998. Spatial firing properties of hippo-
campal CA1 populations in an environment containing two visually

Skaggs WE, Wilson MA, McNaughton BL. 1996. Theta phase precession
in hippocampal neuronal populations and the compression of temporal

Squire LR, Shimamura AP, Amaral DG. 1989. Memory and hippocam-

impaired coding of novel environmental cues. J Neurosci 17:5167–
5174.

Touretzky DS, Redish AD. 1996. A theory of redent navigation based on

Tovee MJ, Rolls ET, Treves A, Bellis RP. 1993. Information encoding and
the response of single neurons in the primetemoral visual cortex. J

Treves A. 1990. Graded-response neurons and information encodings in

Vanderwolf CH. 1969. Hippocampal electrical activity and voluntary

Wallenstein GV, Hasselmo ME. 1997. Gaegaic modulation of hippo-
campal population activity: sequence learning, place field development,
and the phase precession effect. J Neurophysiol 78:393–408.

Wilson MA, McNaughton BL. 1993. Dynamics of the hippocampal

Wilson MA, McNaughton BL. 1994. Reactivation of hippocampal

Zheng K, Ginzburg I, McNaughton BL, Sjövold TJ. 1998. Interpre-
ting neuronal population activity by reconstruction: unified frame-
work with application to hippocampal place cells. J Neurosci
79:1017–1044.

Behav Neurosci 99:1006–1018.