
**THE NEURAL BASIS OF
NAVIGATION**
Evidence from Single Cell Recording

edited by

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PREFACE

THE STUDY OF NAVIGATION-RELATED NEURAL ACTIVITY BEGAN WITH THE DISCOVERY OF HIPPOCAMPAL PLACE CELLS

The investigation of navigation-related neural firing patterns began with the landmark studies of John O'Keefe and colleagues (e.g. O'Keefe, 1976; O'Keefe & Dostrovsky, 1971). These workers were interested in the nature of hippocampal mnemonic function, and they approached this question using what was, at the time, a quite novel approach. Rather than just lesioning the hippocampus to see what an animal could remember after the hippocampus was gone, they instead implanted small electrodes into the hippocampi of rats, so that they could "eves-drop" on the firing patterns of individual cells. They then recorded from these cells as the rats freely explored an environment in which they encountered food, liquid, and other objects.

One salient aspect of these observations was that many of the cells showed location-specific activity. That is, an individual cell was active at high rates when the animal visited a particular, circumscribed region of space, and was virtually silent any other time. Each cell had its own preferred region, so that for each location the rat could occupy, there was a unique pattern of hippocampal activity.

Figure 1 provides an illustration of this Place Cell phenomenon. Figure 1A shows a recording paradigm first developed by Muller et al., (1987) and which has been widely used to study the spatial firing properties of these cells. In this paradigm, the rats constantly forage for tiny food pellets which are dropped from an overhead dispenser at a rate of about one every 30 seconds. Pellets dropped in this way fall to random locations throughout the floor of the high-walled cylindrical recording chamber. Rats search for these pellets using a locomotor pattern in which they constantly move in an apparently random pattern of varying trajectories with which they repeatedly cover each portion of the cylinder floor. The momentary position of the rat is constantly monitored by an overhead video tracking system. The rats are chronically implanted with micro-recording electrodes used to detect the occurrence of action potentials in the cell(s) of interest. The cells are recorded during sessions lasting from 15 min to 1 hour while the rats constantly forage. After the session is complete, the recorded action potentials and position records can be used to generate a firing rate map, which indicates the average rate of the cell at each location within the cylinder.

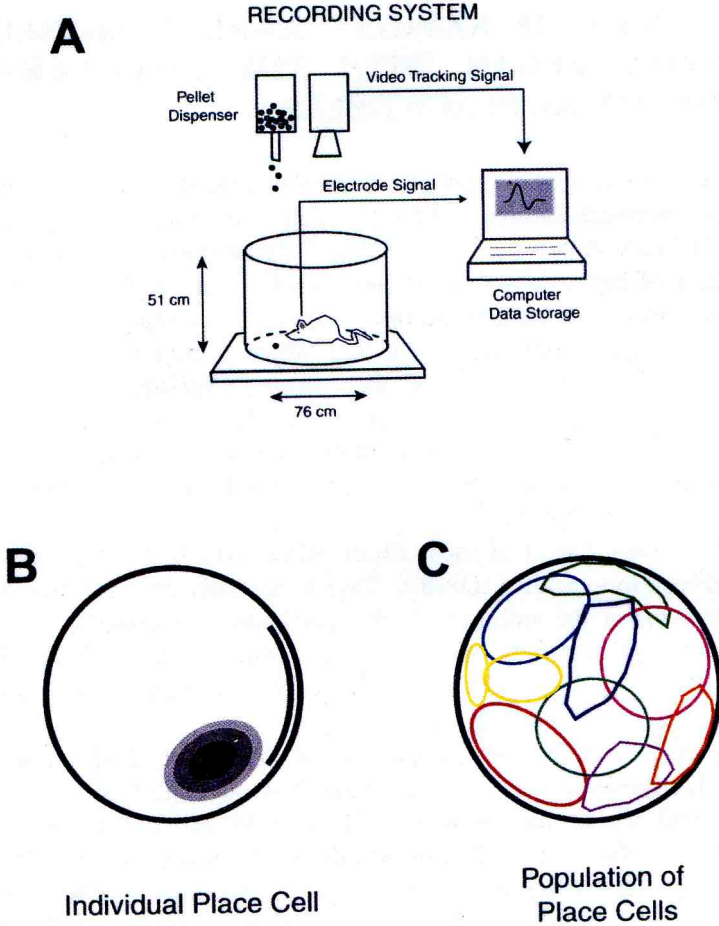


Figure 1. Place Cell phenomenon. A. Behavioral paradigm and recording system used for many investigations of Place Cells (see text). B. Overhead view of the recording chamber floor. The arc along the inner edge at 3:00 O'clock indicates the position of a white cue card used in many experiments as an orienting cue. The darkened oval region indicates the area in which the cell was active, with darker shading representing higher average rates. C. A set of several place fields recorded from the same animal. The location, shape and size of the field for each cell is indicated using a different color.

An idealized version of a typical hippocampal Place Cell is shown in Figure 1B. The cell fired at high rates whenever the rat was within an oval-shaped region located in the lower, right portion of the cylinder. Darker shading indicates higher rates. This diagram illustrates a typical observation that the cells show the highest rates in the center of the firing field, and the rates taper off surrounding this, thus forming a bull's-eye

pattern. The cell is virtually silent whenever the rat is located outside this area.

Figure 1C shows a schematic representation of results from recordings of a large number of hippocampal cells in one animal. The outline of the place field for each cell is indicated by a different color. Note that each cell's place field has a different location, as well as a different size and shape. This illustrates that, together, the population of hippocampal Place Cells covers the entire floor of the cylinder, so that for each position the rat occupies, there is a unique pattern of activity in the hippocampal cell population.

One possible explanation for the activity of these cells could be that each cell is simply driven by some sensory input available from its preferred region (such as an odor, or a particular view of the experimenter-placed cue card). Early work from the O'Keefe laboratory, however, made it clear that, although the cells are influenced by environmental cues, the complete explanation could not be that simple. As reviewed in Chapters 1, 2, and 3, the cells, instead, show an uncanny ability to track the animal's position even when the salient environmental cues are removed, or are ambiguous. As identified in early work by O'Keefe and Nadel (O'Keefe, 1976; O'Keefe and Nadel, 1978) this ability relies, at least in part, on a process known as path integration, or dead reckoning, in which the animal uses its own movement through space to track (integrate) its current position.

This astonishing finding suggested to O'Keefe and Nadel that the main function of the hippocampus was to provide a cognitive map of the animal's environment. In their landmark book, "The Hippocampus as a Cognitive Map" (O'Keefe and Nadel, 1978) they reasoned that the hippocampus provided the machinery to generate an abstract representation of the animal's spatial surroundings, using a path integration process. They further reasoned that this postulated spatial mapping function could provide an explanation for much of the literature on the effects of hippocampal lesions on memory. First, many of the tasks for which performance was affected by hippocampal damage were spatial tasks. In addition, O'Keefe and Nadel argued that even hippocampal lesion-induced impairments on tasks which were not obviously spatial could be explained by the idea that a spatial mapping ability was central to some aspect of the solution of that task. In Chapter 13, Nadel and Payne offer an updated version of this view.

The idea that the sole function of the hippocampus is to provide a cognitive map was controversial when it was initially proposed, and has remained so to the present day. Some workers still adhere to the idea that hippocampal function is primarily spatial in nature. Others, however, believe that the hippocampus also incorporates non-spatial information,

so that it forms a more general memory system. This controversy is illustrated by Chapter 6, in which Dudchenko, Wood & Eichenbaum review data showing that hippocampal cells are influenced by non-spatial, as well as spatial variables.

SINCE THE INITIAL DISCOVERY OF PLACE CELLS IN THE HIPPOCAMPUS, INTERESTING, ABSTRACT SPATIAL SIGNALS HAVE BEEN DISCOVERED THROUGHOUT MANY OTHER PORTIONS OF THE RAT'S LIMBIC SYSTEM

Following the documentation of Place Cells in the hippocampus proper, several investigators, beginning in the 1980's, began to venture out of the hippocampus to look for navigational signals in areas which are anatomically interconnected with the hippocampus (e.g. Ranck 1984; Barnes et al., 1990; Quirk et al., 1992). Interestingly, cells in numerous additional limbic system areas have also been found to contain robust spatial signals (see Figure 3 below).

IN ADDITION TO PLACE CELLS, THE RAT LIMBIC SYSTEM ALSO CONTAINS A TYPE OF CELL KNOWN AS HEAD DIRECTION CELLS

One seminal finding from these extra-hippocampal recordings was the discovery of a cell type known as Head Direction Cells, recorded initially by Ranck (1984), in the postsubicular region of the subicular complex. These cells receive their name from the fact that each cell fires whenever the rat's head faces a certain direction in relation to the surrounding environment. Each Head Direction Cell fires at high rates whenever the rat faces one particular direction (over an approximately 90 degree range), and is silent any time the rat faces a different direction. Each cell has its own preferred direction.

Figure 2 illustrates this directional firing phenomenon. Figure 2A shows an overhead view of the cylindrical recording chamber used in the Muller et al. (1987) recording paradigm (as in Figure 1) which has been used for many studies of these Head Direction Cells, as well as the Place Cells. The numbers around the outside show the convention used to assign heading direction values along the range from 0 to 360. When Head Direction Cells are studied in this paradigm, the rat is equipped with

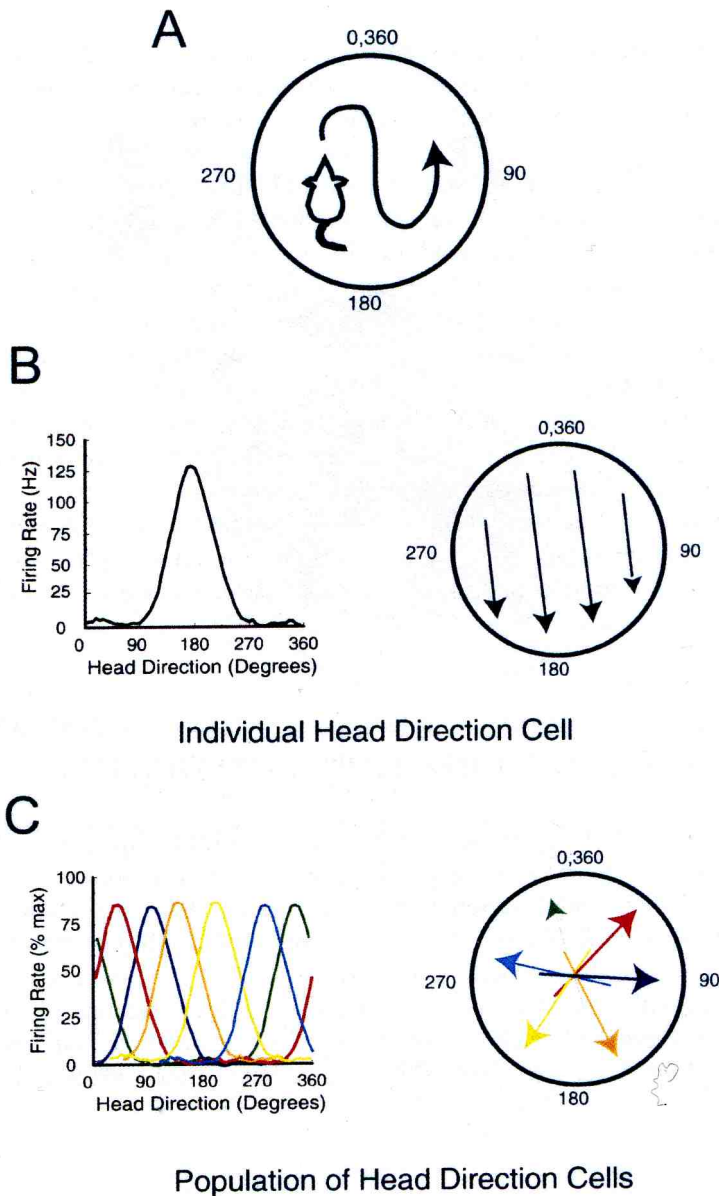


Figure 2. Head Direction Cell phenomenon. A Overhead view of the cylindrical recording chamber showing the convention used to assign numeric values to all possible directional headings. B. Left: Directional tuning function for a typical postsubicular Head Direction Cell. This shows average firing rate as a function of directional heading recorded during a pellet-chasing session (see Figure 1). Right: Schematic representation of directional firing. The cell fires whenever the rat's head is aligned with the set of parallel lines. C. Same as B, but directional firing properties are shown for a population of Head Direction Cells recorded from the same animal.

a set of two headlights, rigidly attached to the animal's head, with one toward the front, and one toward the back of the head (not shown). This enables the overhead tracking system to determine the rat's exact directional heading.

Unlike the Place Cells, the activity of the Head Direction Cells is not influenced by the location of the animal; the cell is equally likely to fire at high rates from any location within the cylinder. Instead, the cells fire optimally whenever the rat faces in one particular direction within the cylinder. Specifically, any time the rat's head is aligned along a particular set of imaginary parallel lines, the cell will fire. Figure 2B shows a schematic illustration of this type of firing using an overhead view of the cylinder floor. Also shown is a typical directional tuning curve for a Head Direction Cell recorded from the postsubiculum. Note that the cell fires as a roughly triangular, or Gaussian function of directional heading.

Figure 2C illustrates that different Head Direction Cells have different preferred directions, so that for any possible direction the rat can face, there will be a unique pattern in the Head Direction Cell population to signal that direction.

CELLS IN SOME AREAS SHOW COMBINED INFLUENCES OF DIRECTION AND LOCATION

In addition to these Head Direction Cells, and the Place Cells already discussed, there have been found cells in a number of regions which show both directional and locational influences (e.g. Sharp & Green, 1994; Sharp, 1996, Cho & Sharp, 2001). For example, the cell may fire more in some locations than others, but may also show a broad directional preference within these areas. These combined place and directional cells have not received much attention, and, in general, it has become customary to focus on cells which are clearly either place-related or direction-related.

HEAD DIRECTION CELLS AND PLACE CELLS ARE LOCATED THROUGHOUT MUCH OF THE RAT LIMBIC SYSTEM

Cortical Areas Containing Navigation-Related Signals

Figure 3 provides a schematic diagram of many of the areas in which Place Cells and Head Direction Cells have been discovered. This, of course, includes the hippocampal formation, which consists of the hippocampus proper, the dentate gyrus (not indicated in figure), and the

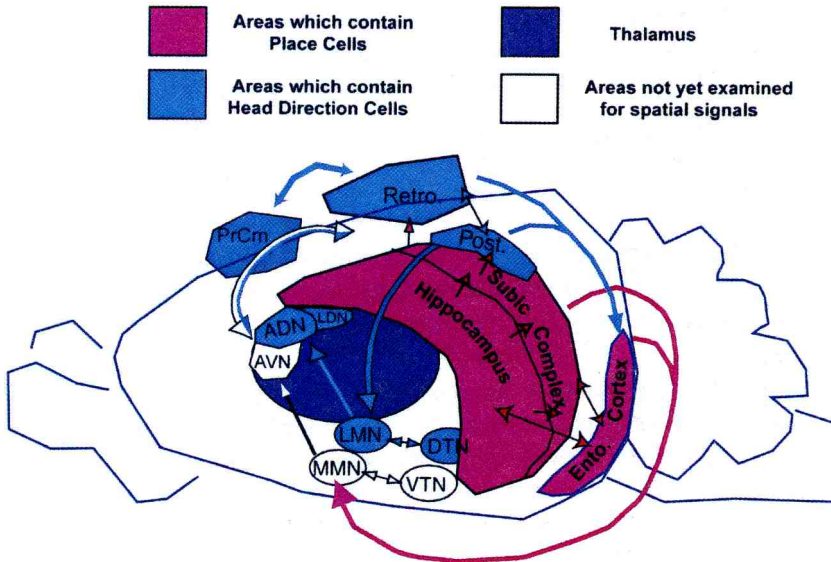


Figure 3. Anatomical connections of the limbic system areas known to contain navigation-related spatial signals (see text). ADN; anterodorsal thalamic nucleus, AVN; anteroventral thalamic nucleus, DTN; dorsal tegmental nucleus, LDN; laterodorsal thalamic nucleus, LMN; lateral mammillary nucleus, MMN; medial mammillary nucleus, Post; postsubicular cortex, PrCm; medial precentral nucleus, Retro; retrosplenial cortex, VTN; ventral tegmental nucleus.

subiculum (Witter et al., 2000). It also includes the additional (besides the subiculum) members of the subicular complex; specifically, the presubiculum, postsubiculum (also referred to as dorsal presubiculum), and parasubiculum. In this diagram, the subiculum, presubiculum, and parasubiculum have been grouped together within the structure labeled subicular complex. The postsubiculum is also included in this complex, but is designated separately.

As already discussed, Place Cells were initially documented in the hippocampus proper (O'Keefe, 1976; O'Keefe & Dostrovsky, 1971). Since then, cells with location-related firing properties have also been discovered in the dentate gyrus (Jung & McNaughton, 1993), the subiculum (Barnes et al., 1990; Sharp & Green, 1994; see Chapter 7), and the parasubiculum (Taube, 1995). In addition, Place Cells have been recorded in the entorhinal cortex (Barnes et al., 1990; Mizumori, Ward

& Lavoie., 1992; Quirk et al., 1992; see Chapter 6), which serves as a major cortical input/output structure for the hippocampal formation.

The major connections of these areas (as outlined by Witter 1989; Naber et al., 2000) are indicated in Figure 3, and it can be seen that these Place Cell-containing areas are all closely interconnected.

Head Direction Cells were initially discovered in the postsubicular component of the subicular complex (Ranck 1984; Taube et al. 1990). Since then, they have also been documented in the retrosplenial area of the cortex (Chen et al., 1994; Cho & Sharp, 2001). Note, the postsubiculum and retrosplenial cortex are strongly, reciprocally connected anatomically (Wyss & van Groen, 1992). Most recently, Head Direction Cells have also been discovered in the medial precentral nucleus (anterior cingulate cortex), as presented by Mizumori et al. in Chapter 11.

Note also that there is opportunity for “cross-talk” between these cortical Head Direction and Place Cell-containing regions. For example, the subiculum projects to the postsubiculum (van Groen & Wyss, 1990), as well as the retrosplenial cortex (Wyss & van Groen, 1992). In turn, the postsubiculum and retrosplenial cortex project to the entorhinal cortex (Burwell & Amaral, 1998; van Groen & Wyss, 1990; Wyss & van Groen, 1992).

Subcortical Areas Containing Navigation-Related Signals

In addition to the cortico-cortical connections between these areas, many of these regions also participate in a subcortical loop similar to that discussed by Papez (1937) and thought, at that time, to have to do with emotional information processing. In general, this loop consists of: 1) a projection from limbic cortical areas down to the mammillary bodies of the hypothalamus, 2) a projection from the mammillary bodies to the anterior thalamus, and 3) a reciprocal connection back to the limbic cortex.

Detailed investigation of this loop has revealed that it actually consists of three separate, parallel sub-loops (Seki & Zyo, 1984; Shibata, 1992; see review by Allen & Hopkins, 1989). One of these sub-loops consists of a projection from the prefrontal components of the limbic cortex, preferentially down to the pars medianus of the medial mammillary nucleus, up to the anteromedial nucleus of the anterior thalamus, and back to prefrontal regions. Since this component of the Papez circuit has not (yet) been implicated in navigation-related information processing, it is not shown in Figure 3.

The second sub-loop of the Papez circuit consists of a projection from the postsubicular cortex (Post.) down to the lateral mammillary nucleus (LMN) of the mammillary bodies and then up to the anterodoral

nucleus (ADN) of the anterior thalamus, and, finally, a broad, distributed, reciprocal projection back to several regions of limbic cortex, including the post, pre, and parasubiculum, and entorhinal and retrosplenial cortices (Allen & Hopkins, 1989; Seki & Zyo, 1984; Shibata, 1989, 1992, 1993; Spripanidkulchai & Wyss, 1986; Thompson & Robertson, 1987; Van Groen & Wyss, 1990, 1992). Interestingly, each of the subcortical nuclei in this component of the loop are areas in which Head Direction Cells (but not Place Cells) have been discovered (Blair & Sharp, 1995; Blair, Lipscomb & Sharp 1997; Stackman & Taube, 1998; Taube, 1995; see Chapter 9). Thus, it appears that the subcortical components of this sub-loop, (as well as the postsubiculum, which provides the main cortical input to this sub-loop) are specialized for calculating and/or transmitting head direction information.

The third sub-loop of the Papez circuit consists of a projection from the subiculum and entorhinal cortex down to the medial mammillary nucleus (MMN) of the mammillary bodies, then up to the anteroventral nucleus (AVN) of the thalamus, and back to the retrosplenial cortex, entorhinal cortex, and all components of the subicular complex (Allen & Hopkins, 1989; Seki & Zyo, 1984; Shibata, 1988, 1989, 1992, 1993; Spripanidkulchai & Wyss, 1986; Thompson & Robertson, 1987). It is not yet known what, if any, spatial signals are present in the subcortical areas of this component of the circuit of Papez. However, given the fact that the cortical limbic areas involved in this loop (subiculum and entorhinal cortex) most prominently are those which contain Place Cells, this suggests the possibility that the subcortical nuclei may also contain Place Cells.

Finally, each of the LMN and MMN have one major input in addition to their respective limbic cortical afferents. Specifically, the LMN is reciprocally connected to the dorsal tegmental nucleus (DTN) of Gudden, while the MMN is reciprocally connected to the ventral tegmental nucleus (VTN) of Gudden (Allen & Hopkins, 1990; Hayakawa & Zyo, 1990; Shibata, 1987). Recent data have shown that, not surprisingly, the DTN also contains Head Direction Cells (Sharp, Tinkelman & Cho, 2001; see Chapter 9). It is not yet known what, if any, spatial signals may be present in the VTN.

It should be noted that Head Direction Cells have also been discovered in the laterodorsal thalamic nucleus (LDN), which appears to form a caudal extension of the ADN, and, like the ADN, is reciprocally connected with limbic cortical areas (Mizumori & Williams, 1993). Also, spatial signals have been recorded from the striatum (Lavioe & Mizumori, 1994; Wiener, 1993), but this has been omitted from Figure 3 for clarity.

PLACE CELLS AND HEAD DIRECTION CELLS LOCATED IN DIFFERENT BRAIN REGIONS SHOW SUBTLE DIFFERENCES IN THEIR SIGNALING PROPERTIES.

Because of the fact that navigation-related spatial signals were first discovered in the hippocampus proper, most of what we know about this general signaling ability has come from studies of this structure. This fact is reflected in the organization of this book, which contains a relatively large number of chapters describing hippocampal cells, relative to those in other brain areas.

However, what data there are from cells in the various other limbic system areas suggests that the cell population within each area shows subtle differences from those in the other regions. These differences in the Place Cells and Head Direction Cells from one area to the next provide clues as to how the various areas may work together to orchestrate the animal's overall navigational abilities.

For example, Chapter 1 (Muller, Poucet & Rivard) and Chapter 2 (Doboli, Minai & Best) both provide reviews showing that the hippocampal spatial maps are highly influenced by the overall environmental and behavioral context, suggesting that the hippocampus may provide spatial information which is highly specific to a given situation. In contrast, evidence reviewed in Chapter 6 (Frank, Brown & Wilson) and Chapter 7 (Sharp) suggest that cells in both the subiculum and entorhinal cortex are more likely to generalize across environments, or even particular trajectories within environments. This suggests that these latter areas may provide spatial information which is more generally applicable.

Chapter 4, by Fenton et al. presents fascinating evidence that the hippocampus may, in particular, be essential when conflicting spatial reference frames are present.

As reviewed in Chapter 9 (Blair & Sharp), the Head Direction Cells within each brain region also show subtle differences from one another, suggesting that they, too, may be somewhat specialized in their role in overall directional coding.

PLACE CELLS AND HEAD DIRECTION CELLS WORK ACCORDING TO SIMILAR PRINCIPLES

Work on Place Cells (mostly those in the hippocampus) and work on Head Direction Cells (mostly from the postsubiculum and anterior thalamus) has suggested that these two cell types work according to

remarkably similar principles. Specifically, both seem to rely, at least in part, on a process known as path integration. As mentioned above, this path integration, or dead reckoning, is the process of updating current locational or directional setting using information about one's own movement.

Thus, for Head Direction Cells, if the animal is, at one point, facing "north", so that Head Direction Cells which code for "north" are active, then, if the animal subsequently makes a 90 degree clockwise turn, this action alone will somehow turn off the "north" cells and turn on the "east" cells. Thus, it appears that the cells can use angular velocity information alone to update the directional firing pattern in the layer of Head Direction Cells. Evidence for this is presented in Chapter 8 by Taube and Chapter 9 by Blair & Sharp.

Similarly, Place Cells appear to use information about translational motion to update the locational signal. For example, as an animal moves from some location X, to some new location Y, located just a few steps west of X, the motion of taking those few steps will somehow turn off the "X" Place Cells, and turn on the "Y" Place Cells. Evidence for this path integration ability in Place Cells is reviewed by Knierim in Chapter 3.

For both Place Cells and Head Direction Cells, it appears that the path integration circuit is also capable of being updated by familiar environmental landmarks. Thus, when repeated recordings are conducted in the same chamber, the Place Cells and Head Direction Cells tend to maintain the same relationship to any available polarizing cues both across and within sessions (see Chapters 1, 2, 3 and 8).

This joint control by both landmarks and path integration is remarkably consistent with introspective evidence about our own navigational abilities. Thus, when one is traveling through a familiar part of town, if one feels momentarily disoriented, it is only necessary to look around for a salient landmark (such as the courthouse) to become re-oriented. However, when traveling, to a new part of town, where there are no familiar landmarks, one is able to keep track of one's position and heading, at least for a while, using just information about one's own movements. Thus, if one leaves the familiar part of town and heads north into new territory for about a mile, then one has a sense of being about one mile north of the start point, even if nothing there looks familiar.

Indeed, evidence reviewed by Rolls (Chapter 10) suggests that the work on navigation-related signals in rats is also highly relevant for primates. Rolls and colleagues have documented cell types which are similar to Place Cells and Head Direction Cells in the primate hippocampal formation.

NEURAL NETWORK MODELS OF THE HEAD DIRECTION AND PLACE CELL SYSTEMS SUGGEST THAT EACH SYSTEM CONSISTS OF AN ATTRACTOR-PATH INTEGRATOR DEVICE.

Neural network models have been developed for both the Place Cells and the Head Direction Cells to attempt to explain the path integration abilities shown by each cell type (McNaughton et al., 1996; Redish, Elga & Touretzky, 1996; Samsonovich & McNaughton, 1997; Sharp, Blair & Brown, 1996; Skaggs et al., 1995; Zhang, 1996). Interestingly, all of these models are remarkably similar in their general properties, although they differ somewhat in the details of their connectivity.

For both Place and Head Direction Cells, the models begin with the idea that the Place (Head Direction) Cell population is linked together via a set of excitatory and inhibitory synaptic connections to form an attractor, so that only one location (direction) can be indicated at any one time.

For the Place Cells (Figure 4; right panel) the cells are, first, imagined as being arranged so that cells meant to represent nearby locations are near to each other (Samsonovich & McNaughton, 1997), so that their place fields form a surface which is isomorphic with the two-dimensional floor of the recording environment. (Note, this is not actually the case; recordings show that two hippocampal cells which are recorded from the same electrode are not likely to have place fields which are close together. However, it is assumed that they are, nonetheless, close to each other in terms of connectivity.) Cells which are close to each other are connected by excitatory synapses, so that they encourage one another to fire. Cells which represent locations far from each other are linked via inhibitory interneurons, so that they are mutually inhibitory. (These excitatory and inhibitory connections have been left out of Figure 4 for clarity.) This attractor network replicates the observed property that, at any one time, the set of Place Cells will stabilize into a firing pattern in which cells meant to represent one particular region are simultaneously active, while those meant to represent all locations outside of this current spot are quiet. Thus, the system cannot take on nonsensical firing patterns indicating that the animal is in two locations at once.

Similarly, Head Direction Cell models (Redish, Elga & Touretzky, 1996; Sharp, Blair & Brown., 1996; Skaggs et al., 1995; Zhang, 1996) begin with the idea that Head Direction Cells meant to represent similar directions are connected by excitatory synapses, while those meant to represent different directions are linked via inhibitory synapses (these connections are omitted from Figure 4). Thus, at any one time, the Head

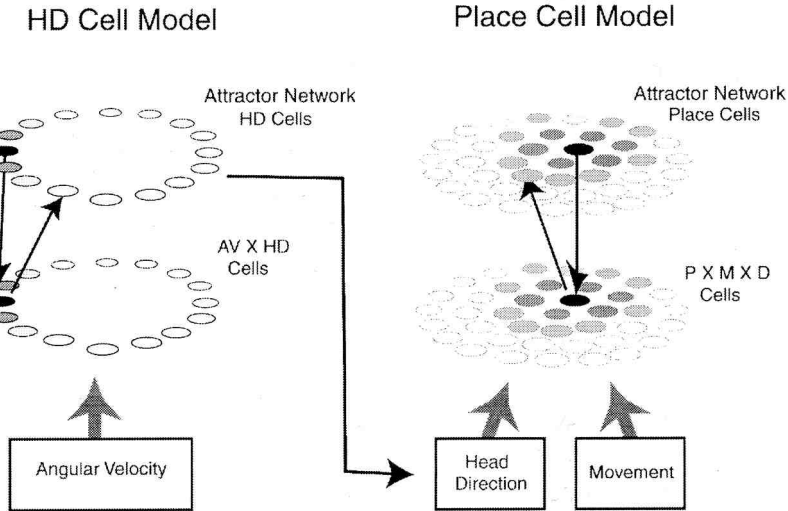


Figure 4. Schematic diagram of neural network models of the Head Direction and Place Cell systems (after McNaughton et al., 1996). See text for further explanation. Each cell's simulated activity level is indicated by a gray scale in which darker shades correspond to higher firing rates. P X M X D; place by movement by direction, AV X HD; angular velocity by head direction.

Direction Cell system will settle into a stable activity pattern in which cells along one, restricted region of the directional range are active, while all other Head Direction Cells are silent. Again, this prevents the system from taking on nonsensical states which would suggest that the rat is facing two or more directions at once.

Next, to replicate the path integration properties of these systems, it is necessary to input information about the animal's movements, and to somehow connect this information with the attractor networks, so that the activity pattern in these attractors is shifted in a way that reflects this movement. For the Head Direction system, the type of movement signal must be that which codes for angular head movement, while for the Place Cell system, the signal must be related to translational movement.

In the Place Cell system, this is accomplished by imagining that the Place Cell attractor network is reciprocally connected with an inner layer which also receives input from movement-related cells, such as motor-command or vestibular signals, that would indicate the current speed of movement (McNaughton et al., 1996). In addition, this inner layer receives input about the rat's current directional heading, such as might be provided by Head Direction Cells. Based on these inputs, the cells in this inner layer will fire in a way which is jointly controlled by the

current setting of the attractor (which indicates the rat's current location), as well as the rat's current movement state and head direction. Note that these three pieces of information are what is needed in order to determine the next location at which the animal will arrive: any one step taken from a given start point and in a given direction will always lead to a single, predictable next location. To accomplish path integration in the attractor network, it is imagined that the Place X Movement X Head Direction Cells in the inner layer project back onto the attractor (Place Cells) with a set of precisely-determined connections, so that each activity state in the inner layer correctly activates the next location in the attractor layer. Thus, the Place X Movement X Direction cell layer constantly updates the locus of activity in the attractor network on the basis of the animal's ongoing movement trajectory. In this way, each Place Cell is called up to fire in exactly the correct location.

In an analogous fashion, the Head Direction Cell system is also imagined to be hooked up to movement-related information via an inner layer (Figure 4; left panel). In this case, that layer receives input about angular head velocity and is also reciprocally connected to the Head Direction Cell attractor network itself. This means that these inner layer cells fire in a way which is jointly determined by the current setting of the attractor network (indicating the rat's current directional heading) and ongoing angular head velocity. Note that these two pieces of information enable a prediction of the next directional heading. For example if the rat is currently facing west, and is in the process of making a 90 degree counterclockwise turn, then the rat will soon be facing south. It is imagined that these Angular Velocity X Head Direction Cells in the inner layer are connected to the Head Direction Cell attractor network in such a way that each activity pattern in this layer causes activity in the appropriate "next" set of Head Direction Cells. Thus, for example, activity in inner layer cells which are active during counterclockwise turns while facing west would send excitatory projections to Head Direction Cells which signal south. In this way, activity in the Head Direction Cell layer is constantly shifted to reflect the animal's ongoing head movements.

As already mentioned, several models of this type have been developed for the Head Direction and Place Cell systems. Computer simulations based on these models have demonstrated that they can actually work to replicate many of the properties of the Head Direction and Place Cells.

IT IS NOT CLEAR WHERE THE PATH INTEGRATION CIRCUITRY IS LOCATED

Figure 3 illustrates that both Place Cells and Head Direction Cells have been discovered in many different brain regions. This raises the question as to which of these areas may contain the path integration circuitry postulated in Figure 4. Evidence and speculation on this question is provided for the Head Direction Cells in Chapter 9, and for the Place Cells in Chapters 7 and 12.

AN EXPANDED VIEW OF THE COGNITIVE MAP

The findings reviewed in this book allow for a considerable amplification and extension of the original hippocampal cognitive map proposal put forward by O'Keefe and Nadel (1978). In retrospect, the amazing findings from the O'Keefe laboratory regarding mapping abilities in the hippocampus were just the tip of the iceberg. Subsequent investigations inspired by this work have led to the discovery of additional types of spatial signals in many limbic regions. Thus, it may now be more appropriate to think of the "cognitive map" as consisting of many of the various components of the rat limbic system all working together to contribute their own aspect of the overall mapping abilities of the animal. A thoughtful review of how these systems may all work together in this way is provided by Touretzky in Chapter 12.

This broader view of the spatial mapping system still leaves numerous unanswered questions. One of these has to do with how this limbic system map is used to actually guide navigational behavior. Insights and relevant data aimed at this question are provided by Mizumori et al. in Chapter 11.

An additional question has to do with the role of the hippocampus itself. With the discovery of so many different brain regions with location-related firing, it is no longer necessary to postulate that the critical circuitry for the path integration itself must reside in the hippocampus proper. It could exist in any one of the other brain regions already discovered to contain Place Cells, or in some as yet uninvestigated region. Thus, the hippocampus itself is relieved of the burden of performing the entire job of mapping, although it is clearly an integral part of the overall circuit. This would seem to provide the possibility that the hippocampal spatial signal could be combined with additional types of information as suggested by evidence presented by Dudchenko, Wood & Eichenbaum in Chapter 5. Thus, as postulated by

Nadel and Payne (Chapter 13) the hippocampal cells may best be viewed as a spatial matrix or “scaffold” on which additional information about specific events may be “hung”.

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