A REVIEW OF THE HIPPOCAMPAL PLACE CELLS

JOHN O'KEEFE

*Cerebral Functions Group, Anatomy Department, University College London,
Gower Street, London WC1E 6BT*

Contents

1. Introduction

Several recent papers have reported the existence of single units in the hippocampus whose firing rate varies as a function of the animal's position in an environment (Best and Ranck, 1975; Hill, 1976, 1978, 1979; Miller and Best, 1978; O'Keefe, 1976; O'Keefe and Conway, 1976, 1978; O'Keefe and Dostrovsky, 1971; Olton *et al.*, 1978). While some authors have called these cells "spatial", we prefer the term "place cells" for reasons which will be set out in Section 2. The place where one of these cells fires is called its "place field".

In addition to the place units, there is another type of single unit which can be recorded in the hippocampus, that of the theta or displace cell. Not much new information has been obtained about these cells since the original descriptions by Ranck and O'Keefe (Feder and Ranck, 1973; O'Keefe, 1976; Ranck, 1973; see also O'Keefe and Nadel, 1978, pp. 197–201). Theta cells can be distinguished from place cells on the basis of anatomical and physiological, as well as functional criteria. In brief these cells have higher firing frequencies and shorter duration action potentials than the place cells, and increase their firing frequency if and only if there is a theta rhythm in the hippocampal EEG. In the rat, these cells increase firing during movements such as walking, running, rearing and exploratory sniffing, but not during eating, drinking, or face washing. In the rabbit, these cells also fire maximally during spatial movements such as walking and running but also fire at an increased rate during immobile arousal and in some cases, during the initial stages of eating. The firing rate during immobile arousal is consistently lower than the rate during walking or running (O'Keefe, unpublished). This is similar to what has been reported for the theta frequency itself (compare Table A6, p. 445 with Table A8(b), p. 450 in O'Keefe and Nadel, 1978).

Ranck has called these cells "theta cells". This has caused some misunderstanding since it has led to the belief that these cells have a special relationship to the slow wave EEG theta not shared by the place cells. This is not so. Both can fire in bursts which are phase locked to a particular part of the theta wave. The difference is that the theta cell does this whenever theta appears in the hippocampal EEG irrespective of the animal's position in the environment. The place cell only shows this bursting firing when there is hippocampal theta *and the animal is in the place field of that cell.*

Many place cells fire with a complex spike burst in which several spikes occur with a short interspike interval (1.5–6 msec) and successive spikes have differing (often decreasing)

amplitudes. Ranck (1973) has called these cells complex spike cells. Theta cells never show this spike configuration.

Fox and Ranck (1975, 1977) have suggested that the complex spike (place) cells are projection (pyramidal and granule) cells whereas the theta cells are probably interneurones. The anatomical distributions of the pyramidal and granule cells correspond to those of the complex spike cells and many of the complex spike cells can be antidromically activated from the areas to which the hippocampus and dentate gyrus are known to project. On the other hand, the theta cell distribution matches that of the interneurones and they cannot be antidromically activated from projection sites.

Others who have studied hippocampal units in the awake animal have not reported finding place cells (e.g. Vinogradova, 1970; Olds et al., 1972; Brown and Horn, 1977; Berger and Thompson, 1978a,b). There are many possible reasons for this failure including the use of cats and rabbits rather than rats in some of the studies, inappropriate environments which severly restrict the amount of spatial information available to the animal, and testing procedures which reduce or restrict the animal's attention to spatial aspects of its environment. In recent unpublished work in our laboratory, we have recorded place cells in the hippocampus of the freely-moving rabbit which are identical to those found in the rat. Furthermore it is much easier to find fields for these cells in a large (8 ft × 4 ft) open pen than in a small 1.5 ft × 1 ft box with high walls.

In this article, I intend to put these controversies to one side for the moment and assume that under the appropriate experimental conditions place cells can be found in the hippocampus of the rat and rabbit. The main aim of the article will be to review what is known about the properties of these cells.

2. What is the Definition of a Place Cell?

Let us start with three examples of place cells. Note that I have changed the figure numbers in the quotes to correspond to those of the present paper. The first is taken from O'Keefe (1976) and is shown in Fig. 1. Recordings were taken while the rat was on an elevated 3-arm maze situated in one corner of the experimental room.

> "Unit 202–1 fired at a high rate when the rat sat in one corner of the window arm (A) but not anywhere else on the maze. The rate was highest when the rat first went to the appropriate place and slowly diminished over time as the animal remained there (compare Fig. 1, 4 and 1). . . . This unit did not increase its firing rate when the animal ate pellets in arm A just adjacent to the preferred place, nor when it drank milk in arm C or water in arm B. No diminution of the response in the appropriate field was observed when a fourth arm was substituted for the original or when all the room lights were turned off except for the red safe light (Fig. 1, 5)." (O'Keefe, 1976, p. 88.)

Our second example is taken from Olton et al. (1978). The corresponding figure here is Fig. 2. They recorded from hippocampal cells while the rat ran from arm to arm of an elevated eight-arm radial maze. The arms were numbered 1 through 8. Food was placed into one of the arms every so often. They classified their place units into different types depending on how many arms and which configuration of arms the unit fired on.

> "Nine of the units had only one arm classified as an on arm whereas the mean rates on all the other arms did not exceed the grand mean. All these type 1 units had a single, well-demarcated area in which the firing rate was increased. An oscillograph record from part of the testing period for one of the type 1 units (no. 11) is presented in Figure 2. The rate of activity was high when the rat visited arm 4, the single on arm, and was low when the rat was on the other seven arms. The increased activity rate occurred as bursts of activity during the visit to arm 4, both on the trip from the center to the end and the trip from the end to the center." (Olton et al., 1978, p. 393.)

Our final example, is taken from a paper by Hill (1978a). Hill recorded place cells in an enclosed automated T-maze made of clear perspex. The rat was trained to alternate between the right and left goal boxes on successive trials. After each run the animal returned to the start box where it awaited the start of the next trial. The rat's passage through the various parts of the apparatus was detected by different photo cell beams. In this experiment, Hill was particularly interested in whether spatial firing was present on the first few trials that the animal ran in the automated T-maze.

"A particularly clear example of first-time spatial firing is given in Figs 3 and 4. The field in this case was a region near the right corner of the choice point (Fig. 3). Spatial firing during the first trial for this rat appears in Fig. 4. During this trial the rat moved out of the start box (a), reached the choice point (b), and turned promptly to the right. Passing through the right arm photocell beam (c) to the goal box (d), it retrieved and consumed a pellet, turned (e), and retraced its path to the start box. Firing of J–11–5 as the rat rounded the corner of the choice point can be seen clearly as the rat moved out and as it returned." (Hill, 1978, p. 290.)

These are good examples of simple place cell firing. The fields can be quite small as in the O'Keefe (1976) example or they can be as large as a whole arm of a maze or even half the environment. As these examples also show, the firing rates when the rat is moving outside the place field are typically low, averaging less than a few spikes per second while the rate in the place field is many times as large. In a quantitative study, Olton et al. (1978) found that the average rate of firing in the on arms was 6.2 spikes/sec while that in the rest of the maze 2.1 spikes/sec.* Hill (1978a) gives figures for the firing rates of 12 place cells. His cumulative averages are 7.0 spikes/sec inside the place fields and 1.0 spikes/sec over the rest of the maze. It should be noted that both of these sets of figures probably underestimate the rate of firing in the place field since, in both studies, the area used to calculate the field rate was usually larger than the actual unit field.

Some place cells fire only when the animal faces in a particular direction within the place field while others increase their rates regardless of the animal's orientation. For these latter cells it is sometimes possible to show that the firing rates are slightly different in the different directions or that the field is larger as the animal traverses it in one rather than another direction, or even more intriguing, that there are subtle shifts in the location of the field when the animal faces in different directions. Although most cells have only one place field in an environment, a few have been recorded which have two or more fields
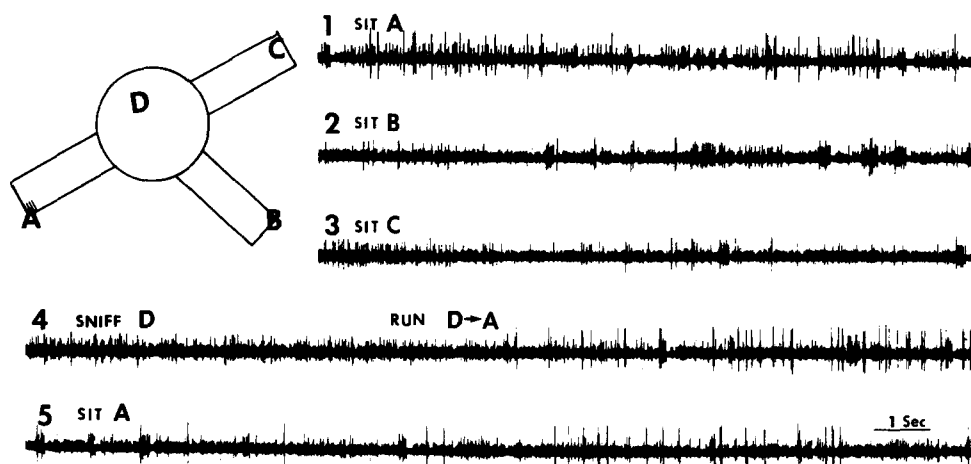

FIG. 1. Place unit. The letters in this and subsequent figures refer to the place on the maze where the behaviour occurred. In this experiment the rat had been made hungry and thirsty, and trained to run to a small porcelain dish wherever it was placed on the elevated T-maze. When placed in arm A, the dish contained three or four 45 mg food pellets, in arm B, water and in arm C, sweet condensed milk. The maze had no walls, maximizing the amount of spatial information available to the animal. Sit does not mean that the animal was totally immobile. The field indicated on the maze is the location of the rat's head during maximal unit firing. Unless there are indications to the contrary (as in 4), the behaviour described at the beginning of the trace continues for the duration of the trace. In this figure there is a smaller displace unit in the background. The record in 1 was taken 45 sec after the record in 4; 5 shows unit activity while the rat sits at A with a new arm substituted for the usual A arm and the room darkened. (From O'Keefe, 1976.)

* Olton et al. (1978) decided whether a given cell was differentially firing on their maze by comparing the rate on each of the arms with an overall mean rate. This gives a conservative estimate of discrimination since the overall rate is inflated by the inclusion of the on arm rates. Using their method of calculation they conclude that each cell has several off arms in addition to one or more on arms. For the present calculations, I have ignored the seven cells which had only off arms and no on arms. The figures given are derived by taking the average of the on arm scores for the remaining 21 of their 28 place cells which had at least one on arm and comparing that with the firing rate for the rest of the arms.
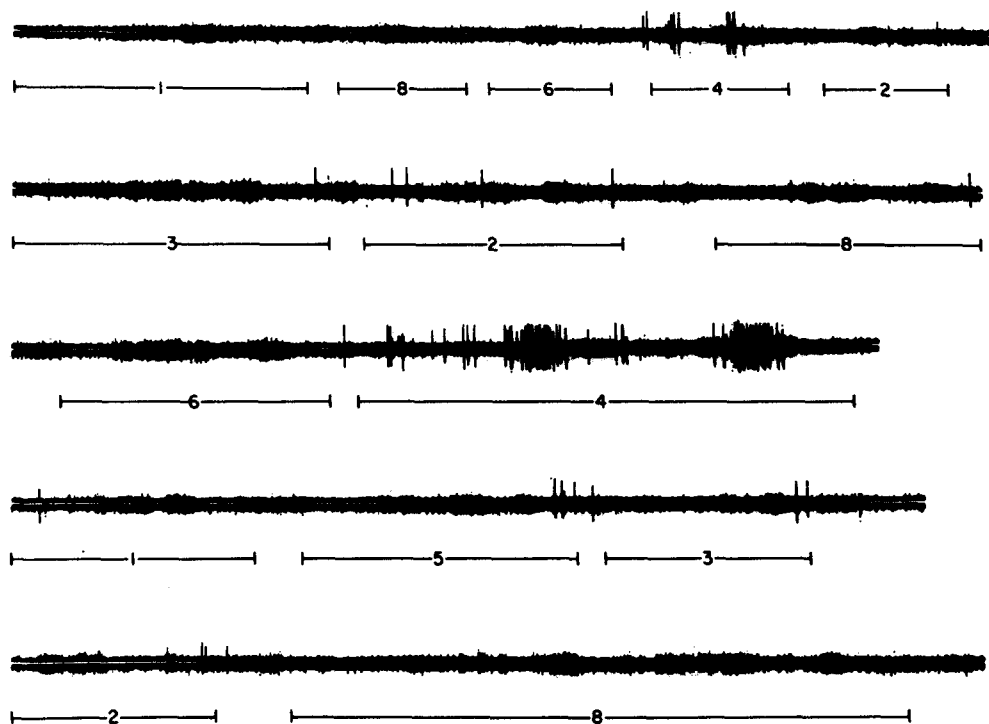
FIG. 2. An oscillograph record from a type 1 unit (No. 11). The numbers underneath the trace indicate the animal's location. Each number indicates an arm; no number indicates the centre platform. Each trace is continuous, so that the animal was entering the arm where the number begins and leaving the arm where the number ends. There are breaks between the traces. Arm 4, where the unit was reliably active, was an "on" arm. (From Olton *et al.*, 1978.)

(Hill, 1978a; O'Keefe, 1976; Olton *et al.*, 1978). While most cells discriminate the place field from the rest of the environment through an increased firing rate there, some appear to have a firing rate in the place field which is significantly below average (Olton *et al.*, 1978). Many cells will fire maximally when the animal first enters the place field and will continue to fire at a lower rate as long as it sits there. Others however will only fire in the place field if the animal is moving. Still others fire maximally when the animal engages in exploratory sniffing within the place field. Of course, none of these behaviours are associated with place cell firing if performed outside of the place field.

How then shall we characterize the class of place cells in order to distinguish them from other cells in the freely moving animal. Notice that I have consistently used the term "place cell" rather than the more general term "spatial cell" used by others (e.g. Olton *et al.*, 1978; Hill, 1978a) in order to distinguish these cells from other types of spatial
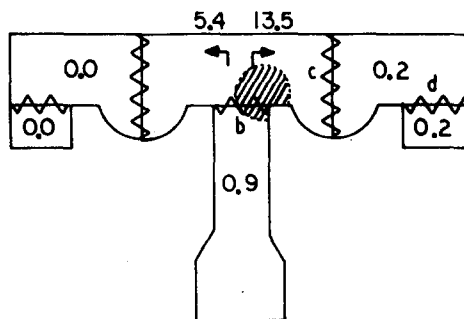

FIG. 3. The field of J-11-5. The cross-hatched region represents the field for this example. The number within each section gives the average firing rate there, in spikes per sec. (After Hill, 1978a.)
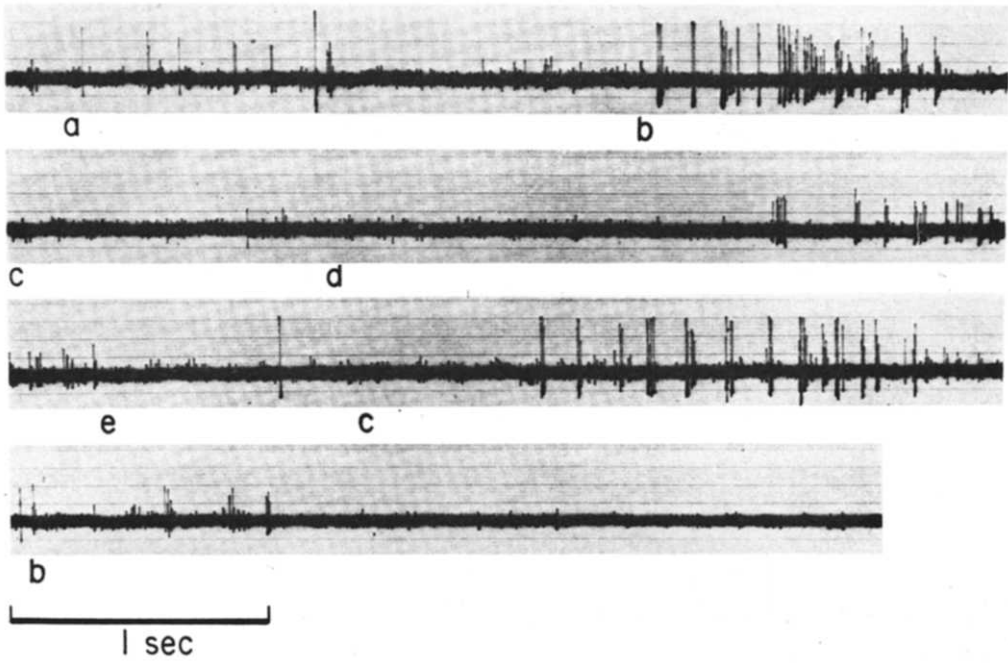
FIG. 4. A striking example of first-time firing in trial 1 for J–11–5. (From Hill, 1978a.)

cells, in particular egocentric spatial cells found in the tectum, frontal neocortex and parietal neocortex (see Section 3 below). There would appear to be at least three definitions of a place cell which differ in the strength of the criteria used.

(a) The weakest definition would include all cells whose firing rate or pattern consistently discriminated between different parts of an environment. It is immediately obvious, however, that such a wide and non-restrictive definition might result in the inclusion of many purely "sensory" cells in the category. For example, a cell which fired in response to a specific odour would differentiate those parts of an environment containing that odour from those that did not and yet we do not want to include such cells in the category of place cell.

(b) A slightly more rigorous definition which would exclude purely sensory cells would be "a place cell is a cell whose firing rate or pattern varies as a function of the animal's location in an environment but can not be shown to be dependent on a single specific sensory input". This definition however, is flawed since it relies on the ultimately impossible task of proving the negative requirement that a cell is not influenced by some unknown sensory input. Since we cannot be confident that we know all of the physical energies that an animal is sensitive to, we cannot accept this as a rigorous definition. Nevertheless it can serve as an adequate working definition. In environments where the sensory cues are not completely under the control of the experimenter, the maintenance of a non-directional place field after visual cues have been excluded by darkening of the room or blindfolding the animals and after the intra-maze cues have been excluded by the rotation of the maze, is a good indication that one is recording from a place cell.

(c) A stronger definition could be based on the results of an experiment by O'Keefe and Conway (1978). They recorded hippocampal cells while the animals performed a place learning task in an environment where the cues for location were identified and controlled. Probe trials in which two of the usual four place cues were available revealed that some of the place cells continued to fire in the place field when any two of the four cues were available. This suggests that the place cell is not "responding" to a particular sensory input but that it receives several redundant cues to the animal's position in an environment. We will discuss this experiment in greater detail in Section 6. A strong definition would require more information about the place cells than exists at this time. The best that one can offer is "a place cell is a cell which constructs the notion of a place in an environment by connecting together several multisensory inputs each of which can be perceived when the animal is in a particular part of an environment".

3. Where in the Brain are the Place Cells Located?

Let us, for the moment, accept a fairly loose criterion for a place cell ((a) above) and ask where we find these cells. The answer is that they have been found in all fields of the hippocampus (CA1, CA3 and FD) and in the medial entorhinal cortex (Mitchell and Ranck, 1977). They have not been reported in other parts of the brain implicated in spatial processing, viz. superior colliculus, parietal cortex, frontal cortex, although other types of spatial cells have been found in these areas. For example, Wickelgren (1971) and Dräger and Hubel (1975) reported that cells in the superior colliculus responded to stimuli in a particular part of egocentric space and that some of these cells will respond to visual or auditory stimuli while others will respond to visual, auditory or tactile stimuli coming from that part of space. Mountcastle et al. (1975) found that cells in area 7 of the monkey parietal cortex fired when the animal reached out into a particular part of space under visual guidance. Because the animal's head was fixed it was not possible to distinguish between egocentric space and space of the environment in this experiment. In unpublished experiments, I have not seen any place cells in the "parietal cortex" (posterior cortex) of the rat but many cells fire selectively when the animal turns its head to one side or towards a particular egocentric direction. Finally, Niki (1974a) has recorded cells in the prefrontal neocortex of the monkey while the animal was performing a delayed alternation task. In

order to obtain reward the animal had to alternate its response from trial to trial, pressing the left key on one trial and then following a delay, the right key on the next, and so on. Niki found that about one-quarter of the cells fired differentially, depending on whether the left or right key was being pressed. Some cells discharged differentially during the delay as well. Niki (1974b) went on to test whether the differential cell responses he observed were due to the position of the key the animal was pressing relative to the other key and the monkey (e.g. its leftness) or whether it was due to the absolute position of the key with respect to the monkey and the testing apparatus. Instead of two keys, he used four keys paired in different ways so that on some trials a key with the same absolute position might be the left key and on others, the right key. He found that while all units showed some sensitivity to the absolute position of the key which was being pressed, a small number also discriminated its relative position. For example, such a cell might fire more to a middle key when it was the left one of a pair than when it was the right one.

While place cells have been found in the medial entorhinal cortex (Mitchell and Ranck, 1977), they have not been reported in the other major source of hippocampal afferents, the septum (Ranck, 1976).

Finally, two studies on hippocampal cells included one or two non-hippocampal cells as controls. Best and Ranck (1975) asked observers to classify cells which were recorded on television tape along with a visual record of the animal's behaviour. The one thalamic cell included was not classified as spatial. Olton et al. (1978) reported that, in contrast to a large majority of their hippocampal cells, neither a neocortical cell nor a thalamic cell had a place field on the eight-arm radial maze.

To conclude then, place cells are found primarily in the hippocampus. They have also been found in one of the major areas connected to the hippocampus, the medial entorhinal cortex. Whether these are "true" place cells in the sense of the stronger definitions given in Section 2 is not known. Equally important is the question of whether these cells receive the place information from the hippocampal place cells or vice versa. Elsewhere we (O'Keefe and Nadel, 1978) have hypothesized that place fields and cognitive maps originate in the hippocampus. If place cells can still be found in the entorhinal cortex after a lesion of the hippocampus then we would have to conclude that the hippocampus receives this information from the entorhinal cortex and does not create it.

4. What Proportion of Hippocampal Cells are Place Cells?

If the large majority of cells in the hippocampus are place cells, then we are forced to seriously entertain the notion that the hippocampus is nothing more than a spatial or cognitive mapping system. On the other hand, if place cells constitute only a minority of hippocampal cells then we should seek for a more global function for the hippocampus which incorporates the existence of place-coded neurones but goes beyond them.

There are considerable difficulties involved in obtaining an accurate estimate of the percentage of different cell types in an area using the single unit recording technique. This is compounded when recordings are taken from freely-moving animals. In most studies there is a large selection factor which biases the sample towards cells which generate large action potentials, have high rates of "spontaneous" activity, and have a morphology which enables them to be held for a reasonable time despite small movements of the electrode relative to the tissue. In the hippocampus this bias appears to operate in favour of the higher frequency theta/displace units and against the low frequency place units. Furthermore, the fact that place units do not have a field in every environment (see below) means that in any given environment, some will not have a field and will be counted as *others*.

Table 1 shows the numbers of the different types of cells reported in the studies which have looked at place units in the freely moving rat. I have divided the studies into those which recorded both complex spike and theta cells and those which have only recorded complex spike cells. We can probably discount the O'Keefe/Dostrovsky study for these purposes since most of their 76 cells were recorded before the place correlate had been discovered. In both the Best and Ranck (1975) and the O'Keefe (1976) study approximately

TABLE 1. NUMBERS OF PLACE CELLS, THETA/DISPLACE CELLS AND OTHERS IN
PAPERS USING THESE OR EQUIVALENT CATEGORIES

Reference	Total cells	Place	Theta	Other
All cells				
O'Keefe and Dostrovsky, 1971	76	8	21	47[a]
Best and Ranck, 1975	19	9	5	5[b]
O'Keefe, 1976	58	29	18	11[c]
Complex spike cells only				
Ranck, 1977	13	13		
O'Keefe and Conway, 1978	34	32		2
Olton *et al.*, 1978	31	28		3
Miller and Best, 1978	15	15		
Hill, 1978a	14	12		
Hill, 1978b	12	12		

[a] Includes 14 cells classified as arousal cells and 2 classified as expectancy.
[b] Includes 2 cells which fired at the end of movements, 1 which fired during drinking and 1 during sniffing.
[c] Includes 5 cells which fired during sniffing, 1 which fired when the rat was picked up in the experimenter's hand and 1 which fired when the rat took a food pellet.

50% of the cells recorded were classified as having a place correlate. As noted above, this probably represents a minimum figure since it overestimates the number of theta/displace cells.

A better estimate can be obtained by carefully mapping the cells according to physiological criteria such as amplitude, frequency of firing and presence or absence of complex spikes. Then, since we know that the place cells are a subset of the complex spike and other slow cells we can try to estimate what this proportion is and arrive at an overall proportion. Fox and Ranck (1975) have mapped the distribution and relative proportions of complex spike, slow, and theta cells. They moved a microelectrode through the hippocampus of the rat in 35.3 micron steps and counted the number of cells at each location. They observed for a long enough time at each point (5 min) to ensure that any cells with very low frequencies would be counted. They concluded that the majority of cells in the hippocampus (58%) were complex spike cells, an additional 9% were slow cells, and only 7% were theta cells. Twenty-six percent were classified as other. Given this distribution, we can ask what percentage of complex spike cells are place cells. In addition to the studies which looked at both complex spike and theta cells, several others first selected complex spike cells and then asked whether they were place-coded. The second half of Table 1 lists the findings in these studies. It is clear that looked at this way the percentage of complex spike cells which are place cells may be as high as 95%. This suggests that place cells constitute the majority of the cells in the hippocampus and as such deserve intensive study since an understanding of their properties will probably take us a long way towards an understanding of the hippocampus as a whole.

5. Are There Differences Amongst the Place Cells in the Different Parts of the Hippocampus?

The hippocampus appears to consist of three basic components, the dentate gyrus, and fields CA3 and CA1 of the hippocampus proper. Although O'Keefe (1976) failed to find simple place cells in the dentate area, they have been reported there by other researchers (e.g. Olton *et al.*, 1978) and in recent unpublished experiments in our laboratory, we have found them there as well. Olton *et al.* (1978) also reported place cells in the CA3 fields. Although it is possible that all of these cells have identical properties, it seems unlikely. O'Keefe and Nadel (1978) suggested that the properties of fully fledged CA1 place cells might be built up in stages. Cells in the earlier part of the circuit (such as the entorhinal cortex and area dentata) might be responding to the conjunction of two or more stimuli

with the appropriate spatial angle between them. Thus they would be place cells only by the weakest definition ((a) Section 2). At subsequent stages of the circuit (such as CA3 and CA1) the inputs from several of these "simple" place cells would be mapped onto the same place cell giving it the ability to identify a part of the environment on the basis of any of several combinations of sensory inputs. This would predict amongst other things, that there would be a much higher proportion of directional place cells in the entorhinal cortex and fascia dentata than in CA3 and CA1. This information is not available yet.

Another difference between the cells in the different parts of the hippocampus concerns the location of misplace cells. These are the place cells which increase their firing rates when the animal is in the place field and doesn't find what it expects there. Either something has been removed or something new has been added. Ranck (1973) called such cells approach-consummate-mismatch cells and reported that they constituted 29% of the cells in the CA1 field as opposed to only 3% in CA3 and 5% in the fascia dentata. It seems reasonable to conclude that the misplace cells are located primarily in CA1.

6. What Causes a Place Cell to Fire in a Particular Part of an Environment?

This is perhaps the most important question one can ask about these cells. There would appear to be three possible answers:

(1) Each cell might be firing in relationship to a particular motor behaviour which the animal performs in one part of the environment and nowhere else.

(2) There might be some stimulus (or pattern of stimuli) which is perceived only from one unique position in an environment.

(3) If (1) and (2) can be ruled out, then one must entertain more complex possibilities. The most obvious of these is that there is a neural system for locating the animal in the environment, a system we have called a cognitive map. It is important to remember that we are concerned here with the factors which cause the place cells to discriminate between different regions of an environment and not with the question of whether there are additional motor or sensory influences on these cells. It is quite clear, for example, that the misplace cells increase their firing rates in the place field markedly when the animal engages in exploratory sniffing there but that the sniffing itself is not the sole determinant of the place field since the same sniffing elsewhere is not accompanied by any place cell firing.

Notice also that if we do conclude that the field of a place unit is due to a behaviour performed in that part of the environment, we would have only changed the problem of environmental influences from a direct immediate one to an indirect one which we would have to eventually deal with: we still need to know what cues the animal uses to identify where in the environment to perform the behaviour. Even were we to find that the behaviour with which the unit firing correlated was embedded in a behaviour chain which was relatively free from immediate environmental influences, there must still be some environmental cue which set off the chain itself. But these are questions of a different nature from the ones which concern us here.

My own conclusions on these questions are that the place cells are *not* firing in a part of the environment because of a behaviour which the animal performs there nor because it experiences a specific stimulus or psychological state there. Both Olton *et al.* (1978) and Hill (1978) also concluded that the firing of the place cells was not correlated with particular behaviours. Ranck (1973) had originally suggested that some of the complex spike cells might be correlated with the animal's behaviour in particular with approach to and consummation of reward. His experimental set-up did not enable him to carry out tests to dissociate the animal's motives for traversing a part of the environment from the mere fact of its doing so. Furthermore his testing situation was rather small and screened off from the testing room which may have reduced the number of place cells active there.

The arguments against the animal's behaviour as an important correlate of hippocampal place unit firing are as follows. In order to rule out an important influence of behaviour and/or psychological state, one can either try to maintain these as constant as possible over the whole environment and show that there is still differential firing in one place or

conversely one can show that wide variations in behaviour or psychological state have only minimal effects on the firing within the place field.

The first observation which is relevant is that many place units will fire if the animal sits quietly in the place field but not if it sits elsewhere in the same environment. While it may be difficult to ensure that an animal behaves similarly in different parts of an environment when it is moving around, it is difficult to believe that a rat would systematically sit differently in different parts of an environment. The best attempt to get an animal to move relatively consistently in different parts of an environment has been the study by Olton et al. (1978). They trained rats on an eight-arm radial maze on a partial reward schedule in which the animal only occasionally received a food pellet at the end of an arm when it went there. This resulted in a fairly constant behaviour pattern where the rat ran from one arm to another in a non-systematic order. Since the rat was not differentially rewarded in any arm we can assume that its expectation was the same in each arm and probably its behaviour as well. Nonetheless, Olton et al. found that 28 of 31 complex spike cells had place fields on the maze.

Finally, in three studies (Hill, 1978a,b; O'Keefe and Conway, 1978) rats have been trained in T-mazes on tasks which required them to make right turns on some trials and left turns on others. In the Hill studies, the rat was trained to alternate: after each trial it had to return to the start arm of the T and, after a delay, go to the other goal arm of the T-maze on the next trial. Furthermore, since the goal box at the end of each arm was set at a 90° angle to the orientation of the goal arm, the rat had to make two consecutive left or right turns to reach it. Thus on some correct trials the rat ran LLRR to go to the goal box and back to the start, while on others it went RRLL. Hill found no evidence that the body turn was an important factor in the place cell firing. For instance a cell with a field in one of the goal arms never showed a double burst of spikes which would be expected if the cell were firing to the (two consecutive) body turns. A non-directional cell with a place field at the choice point fired regardless of the body turn made there (right turn towards the right goal, left turn from the right goal back to the start arm, left turn from the start arm to the left goal, etc.). A similar lack of importance of the body turn as the major determinant of the place field was reported by O'Keefe and Conway (1978). In their T-maze the rat was required to run to the goal, then to the non-goal and finally back to the start arm to complete a trial. The start arm was rotated 180° relative to the crosspiece of the T on some trials so that the animal had to make the opposite turn on those trials to reach the same goal. No influence of the body turn was seen on the place cells. Thus a cell which fired when the rat made a left turn to reach the goal did not fire when it made a left turn to return to the start arm from the non-goal arm. Furthermore such a goal arm cell would typically fire whether the rate made a right turn or a left turn to reach the goal arm. Notice also that in the Hill studies and the O'Keefe and Conway study the role of reward on place field firing was minimal. For example, Hill (1978b) reported that several directional place cells fired only as they returned to the start box away from the goal boxes. O'Keefe and Conway (1978) reported that of twenty-five cells with place fields on their T-maze, five had place fields in the non-goal arm where the rat never received reward. We can conclude from these studies that it is unlikely that either body movements or the presence of reward are the major determinants of the firing of a place cell in a particular part of an environment.

Another approach to the same problem is to see whether different behaviours within the place field or different motivations for going there have any influence on the unit firing. In our experience the animal's behaviour in the place field has minimal influence on cell firing. In his unpublished thesis, Hill (1979) came to the same conclusion.

"Spatial firing is remarkably independent of the animal's behaviour within the unit's field. Occasionally, firing is specific to a particular orientation of the animal, so that certain movements seem to elicit higher firing rates. Yet the same movements do not produce higher firing rates in other parts of the environment or when they take the animal to some other orientation within the field. In some cases, maximal spatial firing seems to occur only when the rat sniffs vigorously at a certain part of the field. In most cases, however, spatial firing occurs reliably whenever the rat is within the field, whether the rat is passing through, exploring, sitting quietly, eating or grooming." (Hill, 1979, pp. 16–17.)

Best and Ranck (1975) reported that five of the nine place cells in their study were judged to fire fastest when the animal made a particular movement at or towards a specific place. At this point it is not clear whether these were directional place cells or whether some place cells do signal information about the animal's movements in addition to its place in the environment.

We have come to a similar conclusion about the role of motivation in the place cell firing. In both the rat and rabbit, it seems to matter little whether the animal goes into the place field "spontaneously", to obtain a reward such as food, to avoid punishment, or is forcibly held there by the experimenter (which is aversive for rabbits). Ranck (1977) has recently recorded place units from female rats with pups in a "family" box. He finds that cells fire in a part of the box whether the animal goes there to get food, to get water, to retrieve a pup, for non-specific exploration, or if the rat is picked up and placed there by the experimenter. O'Keefe (1976) reported that in a T-maze in which the rat had been taught to expect different rewards in different arms, food in one, water in a second, and sweet milk in the third, there was no change in unit firing in the place field on a particular arm when the animal was retrained to expect a different reward on that arm.

Finally, in unpublished experiments, I have observed these place units under circumstances which would appear to minimize the role of motivation and reward. The rats had never been deprived of food or water and had not been rewarded in the testing situation. Similarly in the O'Keefe and Conway (1978) study, hippocampal units were studied in two environments. One was a small elevated platform where the animal was never rewarded while the other was an elevated T-maze within a set of black curtains where the rat was rewarded for going to a goal arm as defined by four controlled spatial cues and also rewarded for subsequently returning to the start arm. As many cells had fields in the former environment as in the latter. While it might be argued that there was some secondary reward associated with the small platform since the animal was consistently taken from there into the cue-controlled environment where it was rewarded, this should not have as much influence as the primary reward in the other situation.

In summary then, place units do not appear to fire in a part of the environment primarily because of something the animal does there or, because of its motivation for going to that part of the environment. Rather, they appear to be primarily cognitive, signalling the animal's position within an environment irrespective of its behaviour and motivational state or the reward properties of that place. That is not to say that we have ruled out all influences of these factors but only that such influences are not the primary determinant of unit firing. If they exist they will require much more subtle analysis than has been performed thus far.

7. What are the Environmental Determinants of Firing in the Place Field?

If neither the animal's motivation nor other psychological states nor its behaviour, makes any substantial contribution to the cell firing in the place field, then we can turn our attention to the environmental influences which determine where the cell fires. The important questions are: What are the sensory cues which cause the cell to fire in a particular place? Is there a single cue or are there several? Are particular combinations of cues necessary or are many of the cues redundant?

There are two different methodological approaches to the study of sensory inputs to a neurone. The first is the classical approach which has proved relatively successful in the study of the sensory systems, in particular the visual system (Hubel and Wiesel, 1962). Here the animal is held stationary, successive stimuli are presented to it, and the neural response to each presentation registered. Stimuli can be moving or stationary, simple or complex, alone or in combinations. This approach works reasonably well when one has a good idea beforehand what the range of possible stimuli might be as in the sensory pathways. Once one moves to areas more distant from the periphery, the method becomes inefficient and in the case of limbic structures in general and the hippocampus in particular,

not notably successful. The alternative approach is to look for consistent unit firing in a sensory rich environment and then to manipulate the environment in an attempt to isolate the cue or cues responsible for the unit firing. This is part of what we have called the neuroethological approach. A fuller description of these two approaches can be found in O'Keefe and Nadel (1978, pp. 190–196).

Several studies have tried to identify the cues which are responsible for the selective firing in the place field. The techniques that have been used fall into our second class, the neuroethological, and include (a) the rotation or translation of the testing apparatus relative to the rest of the room in order to separate intramaze from extramaze influences, (b) the selective elimination of cues from the environment either through the blocking of one or more sensory modalities or through the physical removal of individual items, (c) the construction of artificial environments within which the cues for spatial location are identified and controlled.

(a) The simplest test for the influence of sensory cues on the place cells is to rotate or translate the testing apparatus relative to the rest of the experimental room. This sets the cues internal to the apparatus, in particular the smells and texture of the floor and the shape of the apparatus, in opposition to the distant external cues. When the rotation experiment is performed on a symmetrical elevated apparatus without walls such as the eight-arm maze, the fields of place cells maintain their spatial relationship to the distant room cues and not to the intramaze cues (Olton et al., 1978; Ranck, 1977; Miller and Best, 1978). In informal observations, I have found a similar place cell reliance on extra-apparatus cues after rotation of a small (40×40 cm) elevated wooden platform. O'Keefe and Conway (1978) used an elevated T-maze in which the physical arms were interchanged from trial-to-trial so that the same arm was used as start, goal or non-goal arm on different trials. They found no influence of the physical arm on unit firing but they did find a strong influence of the distant spatial cues.

There are no reports of the effects of translating the apparatus across the room on the place fields. I have tried this on a few cells which had fields on the small elevated platform and obtained mixed results. For a small number of cells, the field stayed stationary relative to the room cues. For example, a field in the north-east corner of the platform would move towards the south-east corner as the whole platform was translated northwards. Some of these cells would also fire if the platform was removed and the animal held in space where the field originally was. These place fields are clearly determined by extra-apparatus cues.

Many of the cells, however, have a more interesting response to platform translation. They continue to fire in the same part of the box (e.g. the north-east corner) despite translation relative to the room. Some have maintained this field over distances of several metres at which point the field abruptly disappears. Since these fields were not affected by rotation of the platform and are therefore not sensitive to intramaze cues, these findings suggest that the significant extra-apparatus cues may not be very specific but may serve instead to identify parts of the apparatus relative to the room (e.g. this is the corner of the platform nearest the wall or this is the arm of the maze farthest from the light).

These findings should not however be interpreted to mean that only cues distant from the apparatus or testing box can determine the location of place fields. In an extremely important study still in progress, Ranck (1977) is finding that a place cell may be influenced more by the room cues or by the apparatus cues, depending on the type of apparatus (and perhaps the task) on which the rat is tested. He records from the same place cell while the animal is in several different types of testing apparatus, *all of which are located in the same part of the testing room*. The three different apparatuses are: a family box ($29 \times 30 \times 12$ in.) where the mother lives with five pups and builds a next box; an elevated eight-arm radial maze where the animal has learned to retrieve pellets from the ends of the arms without re-entering a previously visited (and therefore empty) arm and a two-lever. Skinner box where she has been trained on a DRL-16 schedule. After the rat is tested in one apparatus, she is removed and another piece of apparatus put in its place. Thus far Ranck has recorded from thirteen complex spike_cells (nine in all three situations) and finds that all thirteen have place fields in the family box and twelve have fields in the eight-

arm maze. The place fields are not so clear in the Skinner box perhaps because of its size or because the rat developed stereotyped behaviours so that it always did the same thing in the same place, making it difficult to dissociate the two. Ranck has tested the effects of rotating the apparatus on the fields of the same place cell in the family box and on the eight-arm radial maze. After rotation, the fields in the eight-arm maze maintain their spatial relation with respect to the room cues while the fields of the same cells keep a constant relation to the family box. Thus the same cell recorded while the animal is in the same part of the room can have a field which relates to the nearby apparatus cues in one testing box or to the distant room cues in another.

(b) A second way of identifying the cues which contribute to place unit firing is to change the sensory inputs by blocking off sensory modalities or by removing or adding individual items to the environment. In an environment with many cues, one should not expect too much success from this latter approach.

In the early paper of O'Keefe and Dostrovsky (1971) they mentioned that they had removed various cues from the environment without affecting the fields of place units. They did find that turning off the room lights abolished the field of one place unit but for the others manipulations such as rotating the platform, turning off various sources of sound or darkening the room had no effect on the field. O'Keefe (1976) came to similar conclusions. Of thirteen place units tested in the dark, eight showed no change in field. Four others failed to fire in the usual field the first time that the animal entered it with the lights out but the field reappeared after interim testing with the lights on. This suggests that the cells were originally responsive to visual stimuli but subsequently switched into some other modality or that the novelty of the testing procedure affected the unit firing on the first lights out trial. Only one of fourteen units showed any change in field when the olfactory/tactile cues on the maze were altered.

O'Keefe (1976) reported that for one carefully studied unit, opening and closing the blind of a window near to the maze changed the place field. With the window blind open, the cell had fields in two of the three arms of the elevated maze. One of these arms was close to the window. The field in the other arm was dependent on the location of the experimenter. The cell fired when the rat entered this arm only if the experimenter was not sitting in his usual place near the end of the arm. When the experimenter returned to his usual place after an absence, the unit continued to fire for the next one or two times the rat entered the arm but then the response "habituated" and could no longer be elicited after the fourth trial. If the experimenter moved position the place field was immediately reinstated. The place field in the arm near the window was not dependent on the experimenter's position but was sensitive to the position of the window blind. When the blind was up, the place field was a small area (approx. 10 cm^2) off the end of the arm, about equidistant from each end corner. When the blind was closed this small field shifted approximately 5 cm laterally, to lie just off the end corner of the same arm. In addition a second larger field appeared in the middle of the same arm. More drastic environmental alterations such as turning off the room lights and substituting a new arm when the blind was closed resulted in unit firing everywhere in the arm nearest the window. These observations suggest that each place cell is receiving many different sensory inputs and that the place field is the resultant of many complex sensory influences, some having a tendency to excite the cell in parts of the environment and others tending to inhibit it. I will discuss this further after the next section.

Hill (1979) tested different environmental changes on the fields of place cells in his automated enclosed T-maze described in Section 2 above. Alterations included: (i) olfactory: cleaning the area containing the place field, covering it with strong odours such as alcohol or cologne, introducing other rats into the place field during the test rat's absence; (ii) visual: changing levels of illumination and the location of light sources, occluding the rat's vision with a mask, covering parts of the maze with cloth; (iii) auditory: adding speaker which emitted clicks near the place field region, altering the acoustical properties of the maze by inserting baffles and doors in various places, opening the top of the maze; (iv) vestibular: spinning the animal at approximately 70 r.p.m. in the start box before the

trial. Finally, (v) the shape of the path was altered by closing doors into parts of the maze or inserting small hurdles or baffles in the rat's path or within the place field. This latter alteration would, of course, also have a marked effect on the animal's behaviour. Hill studied twelve place cells and found that only visual alterations and the insertion of barriers had an influence on any of them. Visual alterations affected three of the twelve units, barriers affected six of ten. None of the other alterations were effective including the drastic one of spinning. As Hill points out elsewhere (Hill, 1978a) the insertion of barriers causes the rat to move through the place field differently so that it may not be exposed to (or attend to) the same aspects of the environment as in the absence of the barriers. In a second study reported in his thesis, Hill (1979) tried to eliminate entire modalities by surgical means. Animals were either blinded, deafened, had their vibrissae removed, or their olfactory receptors destroyed. Place cells were found in all these animals and there were no obvious differences from those found in animals with all their senses intact.

In summary, studies in which the sensory ·aspects of the environment have been manipulated usually fail to significantly influence the unit firing in the place field. In a few instances manipulations have been successful, sometimes resulting in subtle shifts of the field. Although the data are not strong there is a suggestion that changes in the visual inputs (at least initially) are more effective than changes in other sensory modalities. If drastic changes are made to the environment (e.g. by changing visual, olfactory and tactile cues all together), there can be large alterations in place cell firing, often with the cell firing over a much greater area than usual.

(c) The final approach to the problem of identifying the environmental influences on the place cell is to study these cells while the animal is in an artificial environment in which the cues for spatial location are identified and controlled. O'Keefe and Conway (1978) reported an experiment in which this was done. An artificial environment, 215 cm on each side, was constructed using floor-length black curtains as the four walls. Inside this environment there were four cues which the animal could use to locate itself: a light, a white card, a fan and a buzzer. Each one was fixed to the centre of a different wall of the environment. During the experiment the four cues maintained their spatial relationship to each other (for example, the light was always on the wall 90° clockwise to the card), but varied in their location from trial-to-trial with respect to the rest of the experimental room. The rats were trained to go to one arm of a T-maze as defined by its relationship to the four spatial cues. Other means of solving the problem such as using a particular body-turn or intra-maze cues were ruled out by varying the start-arm position from trial-to-trial so that the rat had to make a right turn to reach the goal on some trials and a left turn on others, and by interchanging the arms between trails so that the same physical arm might serve as start, goal, and non-goal on different trials. It was found that rats could learn to get to the goal consistently using the four spatial cues and that place cells recorded in this environment had fields which maintained their spatial relations to the four cues. Furthermore removal of some of the cues on probe trials showed that while some of these place cells were dependent on one or two of the four cues, others maintained their place fields when any two of the four cues were available. These latter units could not be said to be *responding* to any of the cues in the usual sense of the word but appear to be calculating the animal's position in the environment on the basis of several different sets of sensory information. Another interesting facet of these cells was revealed on trials where all four cues were absent. They no longer fired differentially in the place field but fired randomly around the maze emitting more total spikes during this trial than on trials with the spatial cues available. Close examination of the trials on which only two of the four cues were available shows that on some of them there also was an increase in firing in the place field. For some cells which had fields that included the goal area this increase was particularly dramatic on non-reward trials. Taken together these findings suggest that the place fields of some of these cells are due, at least in part, to inhibitory influences which block off the cell firing in parts of the environment other than the place field. We have called these cells "lacuna" place cells.

To summarize this section the available evidence supports the view that the place cells fire in particular parts of an environment because of the cues available to the animal there

and not primarily because of the animal's motives for going to that place, its past experience with rewards or punishments there, or its behaviour in that place. Some units (misplace units) fire maximally in the place field when the animal engages in exploratory sniffing there either because it discovers something new there or fails to find something it expected there. Whether the increased firing rate is related to the sniffing or to the environmental change is not yet clear. The cues for location which the place cells use can be either distant room cues or proximal apparatus cues depending on the situation. They are multimodal but there does seem to be some preference for visual cues. Extensive changes in an environment cause some of these cells to fire over a much wider area than the normal field suggesting that part of the mechanism for constructing the field is an inhibition in areas outside of the field.

8. How is an Environment Mapped onto the Hippocampus?

Once it is accepted that a hippocampal cell can signal that the animal is in a particular part of an environment, it is natural to ask the following questions: Does a collection of such place cells have fields which cover all of the parts of an environment? Do cells representing places in an environment have special neural interactions with each other so that they can be said to form an entity, a map of the environment, or do they remain merely a collection of independent place representations? How many cells in the hippocampus are related to the same place in an environment? If there is a map of an environment in the hippocampus, what is its anatomical shape; as one moves in a particular direction within the hippocampus, do the place fields of an environment change in a systematic fashion? Do the same hippocampal neurones represent places in different environments? If so, are there any common features of the places in the two environments?

Information concerning these questions is relatively sparse, in particular with regard to the connections between place cells representing the same environment. In this section, I will review what we can say at this time.

A microelectrode penetrating through the CA1 pyramidal cell layer encounters successive complex spike cells with only very small movements. At some placements, two cells clearly separable by spike height and waveform can be recorded. In both cases, the electrode must be recording from cells which are in close proximity to each other within the hippocampus. The relationship between the place fields of such close neighbours can tell us something about the representation of an environment within the hippocampus. The most obvious type of systematic relationship which could exist between places in the environment and hippocampal cells which represent those places is an isomorphic topographic one. In such a relationship, neighbouring cells would represent neighbouring positions in the environment and distant cells would represent distant positions. Continuous movements in a direction within the hippocampus would result in systematic orderly changes in the fields in the environment. Something like this seems to be the rule in the sensory analysers of the visual neo-cortex (Hubel and Wiesel, 1963). Unfortunately, the evidence from the spatial cells in the CA1 field thus far does not support this hypothesis (O'Keefe, 1976). Neighbouring cells there are as likely to have fields widely separated in an environment as they are to have ones which are contiguous. Thus it does not seem that the map of an environment within the CA1 field of the hippocampus is isomorphic to the environment which it represents. Similar data are not available for the dentate gyrus or the CA3 field and it is possible that an isomorphic map of the environment might be found in either of these areas or elsewhere. Alternatively, it is possible that the cells representing a particular environment are distributed randomly within the hippocampus and, if there is a map, it is represented by the neural connections between these disparate cells. The connections could be either direct via axon collaterals or through the mediation of interneurones, perhaps the basket cells of Cajal. A random distribution of the place cells representing an environment need not mean that the organization of the hippocampus is random; only that it is organized according to a different principle. One possibility is that there is a systematic change in the potential sensory inputs to the place cells as one moves within

the hippocampus. If an animal attended to different sensory aspects of an environment as it moved from place to place then the cells representing these places would be separated in the hippocampus. On this model, the basket cells would be responsible for selecting the groups of place cells which the successive sensory inputs would activate. This possibility is pursued in greater detail elsewhere (see O'Keefe and Nadel, 1978, pp. 217–230).

Although a systematic isomorphic mapping of an environment has not been found in the CA1 field, it is clear that the fields of a reasonable sample of place cells will cover much of the surface of an environment. The cognitive map theory would predict that this distribution should approach an ideal one in which all parts of the environment are equally represented. Thus far, three of the four studies which have looked at this have found some deviation from this expectation. O'Keefe (1976) reported that there were more fields in the arm of his elevated three-arm maze which faced the experimenter. In their eight-arm radial maze, Olton et al. (1978) found more fields towards one side of the room than the other. O'Keefe and Conway (1978) reported that the place fields on their small symmetrical elevated platform were concentrated around the edges to the detriment of the centre. On the other hand they did find a reasonably equitable distribution on their T-maze inside the cue controlled environment. Hill (1978a) found no tendency for fields to occur in one part of his automated T-maze than in any other. It should be noted that in all four studies the fields have been pooled from cells recorded in several animals. In the O'Keefe (1976) paper, however, the fields from one animal were plotted separately and these also show a slight bias in the same direction as the grouped data. At this stage, it is not possible to say whether these small biases in field positions are due to sampling bias or to some other variable. They clearly are not due to differential rewards or to other preferences the animal might have for one part of the environment over another.

Our final question about the anatomical organization of environments in the hippocampus concerns the relationship between the cells representing places in two different environments. This problem has been approached in two experiments: O'Keefe and Conway (1978) and an ongoing study by Ranck (1977). In both, the same complex spike cell was recorded in two different environments and the fields compared. This is potentially a powerful technique since it can tell us how different environments are mapped in the hippocampus and also perhaps reveal some of the general rules which determine where in an environment a cell will fire. For example, if the same place cell fired in a corner in each of the environments, this might indicate that the stimuli associated with corners were a major input to the cell. O'Keefe and Conway (1978) compared place fields of the same complex spike cells while the rat was on a small elevated platform and while it was performing a place discrimination on an elevated T-maze inside the cue-controlled environment. They reported that fifteen of thirty-four complex spike units had fields in both environments, ten had a field on the T-maze alone, seven on the platform alone and two units did not have a field in either environment. Looked at in another way, twenty-five of thirty-four units had a field on the T-maze, while twenty-five of thirty-four had a field on the small platform. They examined the cells with place fields in both environments to see if there was any systematic relationship between them. None was found. Ranck (1977) has compared the place fields of cells when the rat was in a family box and on an eight-arm radial maze (see Section 7 for a description of this experiment). A comparison of the twelve cells which fired in both environments has not revealed any simple pattern of correspondence. Ranck is cautious about drawing conclusions from these preliminary findings and feels that the number of cells may be too small for any correlations other than very obvious ones to show up. These reservations probably apply to the O'Keefe and Conway (1978) study as well.

Nevertheless, we can draw some tentative conclusions from these two studies. The most obvious is that many complex spike cells have fields in more than one environment. Therefore an environment is not mapped by a unique group of hippocampal cells but instead different environments must use different subsets of the same total pool of cells. The subsets of cells representing two environments would have a substantial overlap. This means that the number of cells in the hippocampus is not a good measure of the amount of information which the hippocampus can contain.

A second tentative conclusion is that there may not be any rules governing the possible places in any environment where a complex spike cell will fire. We should not give up the search for order too quickly but it may be that the hippocampus is a tabula rasa upon which each new environment is written *de novo*. The thought experiment here is one in which an animal is allowed to build two maps of the environment. After the initial map is formed, it is eradicated by some means or other, and the animal is allowed to build a new map of the same environment. Would the two maps look the same? Would the same cells fire in the same places?

9. What Further Information Do We Need to Have About the Hippocampal Place Cells?

The most obvious unanswered question about the place cells is whether the place correlate is the only or even the major correlate of cell firing. Elsewhere (O'Keefe and Nadel, 1978) we have warned against the dangers involved in assuming that hippocampal cells were correlated only with the range of stimuli which the experimenter had chosen. Thus, for example, we suspect that some of the discrepancies between studies might be due to a concentration on the movement correlates of the theta cells in the rat by some authors or the arousal correlates of these cells in the rabbit by others. In a similar fashion, it is possible that the firing of complex spike cells in a particular part of an environment is only part of the total repertoire of behavioural correlates of these cells and that a list of all of these correlates might force us to postulate a function for the hippocampus which is even more abstract than the cognitive map theory. Here I am not thinking so much of complex spatial properties such as those shown by the misplace units or by place cells which only fire in a place the first one or two times that the animal returns (or is returned) there after an absence. Rather, what I have in mind is the possibility that a cell which discharges at a high rate when the animal discovers something changed in a place might also fire when the animal finds a difference in a familiar object or during other types of uncertainty. Such a cell might more properly be described as an uncertainy detector than a misplace cell. To be sure, no-one has yet reported cells with these or similar properties in the hippocampus; the closest is a report by Lynch *et al.* (1978) of preliminary results from unit recordings they did in collaboration with S. A. Deadwyler. They recorded dentate units from rats who had been trained to discriminate between two tones; one tone (S_1) was always followed by food reward while the other (S_2) was not. They found that prolonged bursts of firing were associated with the positive (S^+) tone but only a short burst occurred in response to the negative tone (S^-). Interestingly, no prolonged burst was seen when only one tone was presented and consistently followed by reward. Before we assume that these are some type of uncertainty detector or differential reward cell, it would be useful to know what other behavioural correlates these cells have.

The only non-place correlate which the hippocampal complex spike cells have been consistently reported to have is sleep. Ranck (1973, 1977) has called attention to the fact that these cells will increase their rates when the animal goes into slow wave sleep regardless of where it is in an environment. I agree but do not think much information is transmitted by this increased rate since it is common to most complex spike cells. It is usually assumed that the most probable mode by which the nervous system transmits information is by the differences in firing rates of neighbouring cells. However, maybe this assumption is wrong and there is a special function for these cells during sleep.

The second question which needs much more research concerns the factors determining the firing of a unit in the place field. The O'Keefe and Conway (1978) study indicates that some of these units are multimodal, responding to any subset of the cues in an environment. We need to have answers to two further questions: Are some sensory cues more important than others? Visual cues seem to be more important but are light/dark gradients and shadows more important than point light sources? Another question: Is there another source of positional information than the immediate sensory stimuli impinging on the animal? We have previously suggested that another such source of information might

come from spatial information derived from the animal's movements in an environment (Nadel and O'Keefe, 1974; O'Keefe, 1976; O'Keefe and Nadel, 1978). Hippocampal theta would reflect the use by the hippocampus of this movement-derived spatial information and there is evidence that the frequency of theta during jumping is related to the distance which that movement translates the animal (Morris *et al.*, 1976). If this is so it should be possible to show that a place unit can still identify its place field in the absence of the sensory information normally encountered in that field if the animal is familiar with that environment and has been allowed to locate itself in the environment using the normal sensory cues.

Finally, there are a series of anatomical questions which need answers. (a) Is the map located within the hippocampus or is it constructed elsewhere and merely transferred to the hippocampus? Mitchell and Ranck (1977) have found place cells in the entorhinal cortex but we do not yet have enough information about these to say whether they are on the input or output side of the hippocampus. (b) What are the functions of the various afferent and efferent pathways of the hippocampus? Elsewhere we (O'Keefe and Nadel, 1978) have speculated that the entorhinal cortex–perforant path input conveys sensory information while the septo-hippocampal afferents provide information about the animals spatial displacements. The role of the septum was viewed as transforming information about an animal's movements sent to it from the brainstem into a rhythmical code which specified the distance and direction travelled during those movements. Without this information, existing maps would remain intact but could not be modified to take into account changes in an environment. Maps of new environments could not be constructed. Miller and Best (1978) have reported preliminary results from an experiment designed to study the role of the afferents from the septum and brainstem in place cell firing. They looked at place cells while the rats were performing on the eight-arm radial maze task used by Olton *et al.* (1978) (see above). In addition to normal animals, they recorded from animals with lesions of the fornix, the major afferent (and efferent) fibre system for connections between septum/brainstem and the hippocampus. They found that all fifteen complex spike cells in intact rats had place fields on the maze, as did nine of thirteen cells in the fornix-lesioned rats. The major difference between the two groups, however, was only revealed after maze rotation. While thirteen of the fifteen cells in the intact rats maintained their place fields with respect to the extra-maze cues, only two of the nine place cells in the lesioned animals did so. Most of the cells in these animals showed no relationship to the intra-maze cues either. It would appear from this study that information entering the hippocampus through the fornix is not necessary for maintenance of the place field under stable conditions but is necessary for the hippocampus to successfully cope with environmental changes. More experiments of this type are needed, in particular recordings of hippocampal place units after entorhinal lesions and recordings of entorhinal place units after hippocampal lesions.

(c) Finally, we need to get some idea of what the anatomical shape of a map of an environment looks like. Unless there is an isomorphic map somewhere in the system I do not hold much hope of resolving this problem using electrophysiological techniques. Perhaps the best way to approach it might be to use the newly developed metabolic tracers which label active cells (e.g. Kennedy *et al.*, 1975).

10. Summary

There are two major functional cell types in the hippocampus of rat and rabbit: place cells which signal the animal's position in an environment and theta or displace cells which appear to be related primarily to the animal's movements and in particular to the amount of displacement in the environment which a movement will produce. This paper reviewed the recent literature on the properties of the place units. Some of the conclusions reached are as follows. Place cells probably account for the majority of the units recorded in the hippocampus. The part of the environment where a place unit is active (its *place field*) does not appear to be determined by such factors as the animal's attitude towards that place

or the specific behaviour of the animal in that place. Rather, the place cell is signalling the purely cognitive information that the animal is in a part of an environment. The notion of place is constructed by these cells at least in part on the basis of cues available to the animal at that location.

Experiments indicate that some of these place cells are not responding to particular stimuli but will continue to signal the animal's position in the environment when any one of several different subsets of the total set of spatial cues are available. Locations in an environment do not appear to be mapped onto the hippocampus in any orderly topographic manner. The same hippocampal unit can have place fields in different environments but there does not seem to be any obvious relationship between these fields. It is speculated that connected together in the appropriate fashion these place units could form a spatial map of an environment.

Acknowledgements

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