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SHORT COMMUNICATION
Spatial View Cells in the Primate Hippocampus

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Abstract

Hippocampal function was analysed by making recordings in rhesus monkeys actively walking in the laboratory. In a sample of 352 cells recorded in the hippocampus and parahippocampal cortex, a population of 'spatial view' cells was found to respond when the monkey looked at a part of the environment. The responses of these hippocampal neurons (i) occur to a view of space 'out there', not to the place where the monkey is, (ii) depend on where the monkey is looking, as shown by measuring eye position, (iii) do not encode head direction, and (iv) provide a spatial representation that is allocentric, i.e. in world coordinates. This representation of space 'out there' would be an appropriate part of a primate memory system involved in memories of where in an environment an object was seen, and more generally in the memory of particular events or episodes, for which a spatial component normally provides part of the context.

Damage to the temporal lobe that includes the hippocampal formation or to one of its main connection pathways, the fornix, produces amnesia (Scoville and Milner, 1957; Gaffan and Gaffan, 1991; Squire and Knowlton, 1994). One of the memory deficits in amnesic humans is a major impairment in remembering not just what objects have been seen recently, but also where they have been seen (Smith and Milner, 1981). This type of memory is involved in remembering recent episodes, such as where one saw a person or object, or where one's keys have been left. In experimental studies in monkeys to define the crucial structures to which damage produces memory impairments, it has been shown that hippocampal or fornix damage produces deficits in learning about where objects have been seen (Parkinson *et al.*, 1988; Angeli *et al.*, 1993; Gaffan, 1994).

To analyse how the primate hippocampus operates to help implement this type of memory, we describe here recordings made from single hippocampal neurons in rhesus monkeys actively locomoting in a spatial environment. The aim was to investigate the type of spatial information represented in the hippocampus, to provide a basis for understanding how it could implement a memory for where objects are in a spatial environment. In previous recordings in the primate hippocampus, the monkey was not afforded the opportunity to actively explore (Rolls and O'Mara, 1995). We performed the experiments in the actively locomoting monkey because the spatial properties of rat hippocampal cells are not revealed unless the rat is able to locomote in an environment (Foster *et al.*, 1989). The spatial cells that have been revealed in the rat hippocampus in now classic experiments are place cells, responding when the rat is in a given place (O'Keefe, 1979; Muller *et al.*, 1991). However, these place cells could not mediate at least some of the types of spatial memory in which the primate (including human) hippocampus is implicated, for example a memory of where in space an object has been seen, which can be remembered perfectly even when the human or animal has never been to that particular position in space.

We used a rich testing environment, the open laboratory, to maximize the possibility that many cells with spatial response properties would be found. The monkey could walk round the laboratory in a modified chair on four wheels, the head position and direction (which were the same as those of the walker) were measured every 67 ms with a video tracker (Datawave, Tucson, AZ), and the eye position (horizontal and vertical) was measured with the search coil technique with field coils attached to the chair. The monkeys were extremely mobile in the environment, and reached peak linear velocities of 0.6 m/s and peak angular velocities of 100 degrees/s. The present study is the first in which it has been possible to analyse the responses of primate hippocampal neurons during active locomotion and in a spatially rich environment.

Single neurons were recorded with glass-insulated tungsten microelectrodes with methods that have been described previously (Feigenbaum and Rolls, 1991). The monkey was free to walk with his head in an upright position round an open laboratory in a 2.7 × 2.7 m area in a modified chair on four wheels. Eye position was measured to an accuracy of 1 degree with the search coil technique, with the field coils attached to the walker, to which the head was also attached. The head direction and position in the room were measured using a video tracking device (Datawave) with the camera in the ceiling tracking two light-emitting diodes placed in line 25 cm apart above the monkey's head. We wrote software to provide the position of the monkey's head in the room every 67 ms, the direction of motion of the head, the horizontal and vertical eye position, and from these the position on the wall of the room at

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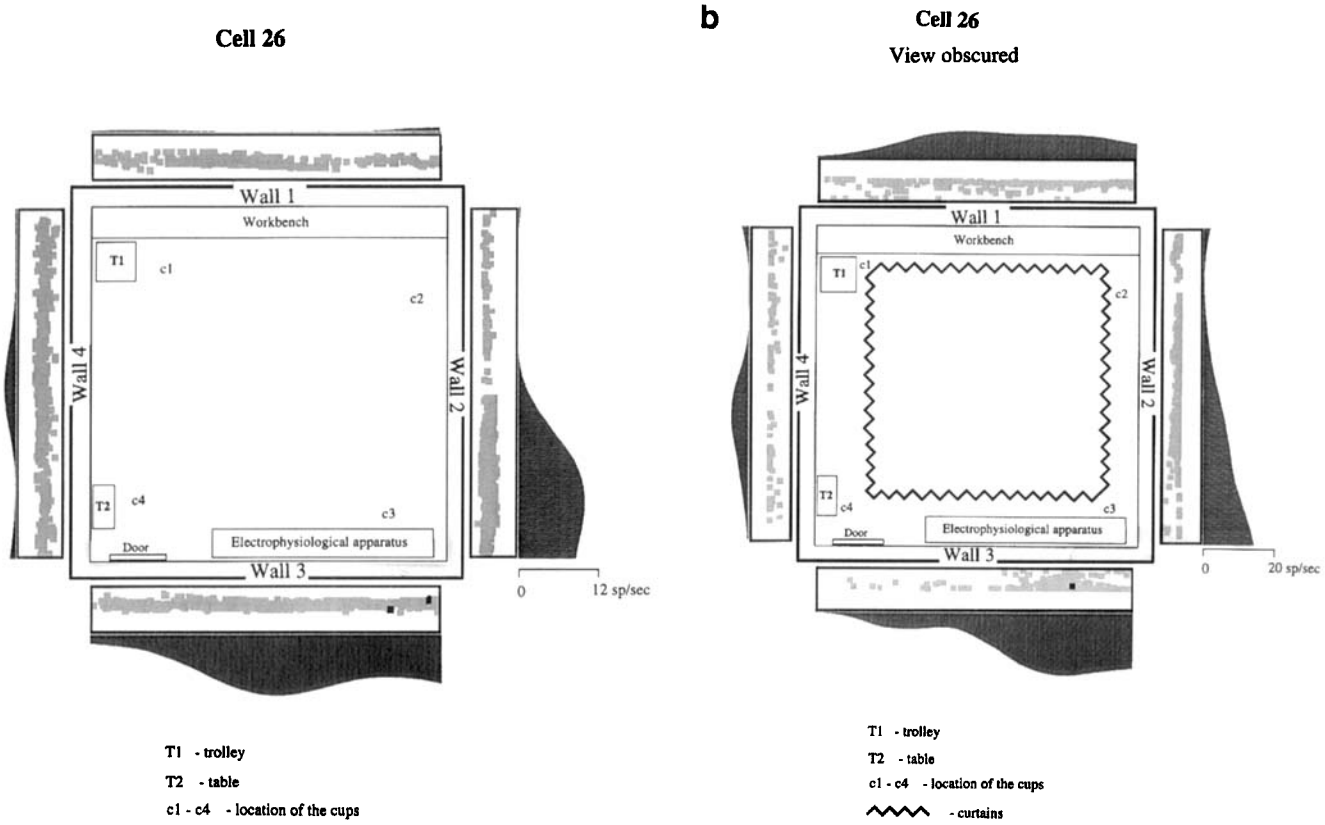

FIG. 1. (a) The spatial view field of a hippocampal pyramidal cell (number 26) during free exploration of the room. The firing rate of the cell (spikes/s) is shown for each wall in the outer set of four panels. A spot on the inner set of four rectangles, each of which represents one of the walls of the room, indicates where on a wall the monkey had been looking every 67 ms during the 7 min recording session shown. The bottom of the wall is represented closest to the centre of the diagram. (b) For the same cell the firing rate is shown when the monkey walked in the room with all the visual details of the four walls obscured by ceiling-to-floor black curtains.

which the monkey was looking. Every time the cell fired the time was recorded to an accuracy of 0.1 ms. The data set for each cell consisted of saved values for the above measurements during periods which were typically between 10 and 90 min, and from these data sets the firing rates and their standard errors were calculated over many 0.5 s periods in which the monkey was looking at the same part of the environment within ±2 degrees. The Datawave spike cutting software was used to ensure that the action potentials of well isolated neurons were analysed. All procedures, including preparative and subsequent ones, were carried out in accordance with the *Guidelines for the Use of Animals in Neuroscience Research* of the Society for Neuroscience, and were licensed under the UK Animals (Scientific Procedures) Act 1986.

The firing rate of a hippocampal pyramidal cell recorded as the monkey was walking round the laboratory is shown in Figure 1a. The firing rate when the monkey was looking at each part of the four walls is shown in the outer panel for each wall. The cell fired fastest (at ~10 spikes/s) when the monkey was looking at wall 3 and at the adjacent part of wall 2. Thus the cell had a spatial view field on wall 3 and part of wall 2. These rates were collected over ~5 min, during which the monkey walked actively through at least 90% of the environment, and looked from different places at the different walls. Evidence that he did look at all parts of the environment is present in the inner set of rectangular boxes, where a spot was placed wherever the monkey fixated a wall of the environment. The cell fired when the monkey looked at the view field from any part of the environment. (Further evidence on this point will be provided in Fig. 2). This type of diagram also indicates the approximate size of many of the spatial view fields found. The spatial view fields of different cells were centred on different walls. Evidence on the size and position of the view fields of all 40 cells analysed is shown in Table 1.

Further analysis of the spatial view fields was possible with the type of experiment shown in Figure 2 for a hippocampal pyramidal cell. The firing rate of the cell is shown in Figure 2a and b when the monkey was stationary at two different places in the environment, and was looking at the spatial environment. The arrow shows the head direction of the monkey, which was fixed for the period of recording in which the firing rates were being measured in Figure 2a and b. The cell fired only when the monkey was looking at a given part of the wall of the room (indicated approximately as the response field of the cell). The firing could not be due to the place where the monkey was, or to the head direction of the monkey, both of which are different in Figure 2a and b. Comparison of panels a and b in Figure 2 shows that when the monkey was closer to the wall (Fig. 2a) the responsive region filled a larger part of the area visible to the monkey, as expected for a response field located on the wall of the room. (In the vertical direction the area visible to the monkey may not have reached the centre of the response field, as shown in Fig. 2a and b). In Figure 2c the firing rate of the same cell (cell 37) is shown when the monkey had been at many different places in the environment, looking in many different directions. Figure 2c also shows that the cell did not fire only when the monkey was at one place, and therefore cannot be described as a place cell. Instead the cell fired whenever

TABLE 1. Properties of the spatial view cells

Cell #	Field	Peak rate (sp/s)	Spont. rate (sp/s)	Location	Recording time (min)	Cell #	Field	Peak rate (sp/s)	Spont. rate (sp/s)	Location	Recording time (min)
1	Corner 3	18.9	0.9	CA1	25	21	Wall 4	16.5	1.7	PSUB	10
2	Corner 1	26	3.8	PSUB	12	22	Cup 4	6	0	PHG	5
3	Corner 3/4	16.2	0.6	CA1	18	23	Wall 1	13.2	0.4	PHG	16
4	Corner 4	11.7	0.5	PHG	4	24	Corner 4	10.5	1	PHG	13
5	Wall 4	19	2.1	CA1	12	25	Cup 4	12	0.5	CA1	33
6	Corner 3	6.9	0.5	CA3	9	26	Corner 3	15	0	CA1	27
7	Corner 4	43.5	0.4	CA3	20	27	Corner 1	4	0.2	CA1	68
8	Corner 1	23.3	0.6	CA3	6	28	Wall 4	7.5	0	CA1	43
9	Corner 4	42	0.7	CA3	5	29	Corner 3	28.5	2.3	PHG	18
10	Corner 3	3.4	0.4	PSUB	8	30	Corner 4	30	0.3	PHG	3
11	Wall 3	17	2.1	CA1	4	31	Corner 1	18	0.3	PHG	3
12	Wall 3	7.5	0	CA1	11	32	Corner 4/door	12	0.3	PHG	6
13	Cup 3/wall 1	8	0	PSUB	14	33	Wall 3	19	0.6	PHG	47
14	Cup 1/cup 3	7.5	0.4	PHG	7	34*	Wall 1/cup 2	13.5	0	CA3	97
15	Corner 1/3	12	0.5	PHG	30	35*	Wall 3/cup 3	21	0	CA3	97
16	Corner 3	14.25	1.2	CA1	7	36*	Corner 1	14.25	0	CA3	26
17	Cup 4	20	0.7	PHG	37	37*	Corner 4	25.5	0	CA3	36
18	Corner 1	8.5	0.1	PSUB	14	38*	Corner 4	6	0	CA1	91
19	Wall 4	7.5	0	PSUB	11	39*	Corner 1	15	0.22	PSUB	37
20	Wall 3/corner 4	6.75	0	PSUB	11	40*	Wall 3	14.25	0.35	CA3	35

Cells 1–33 were recorded from one monkey, and as indicated by the asterisk, cells 34–40 were recorded from the second monkey.

the monkey looked at a certain part of the environment, which is termed the spatial view field of the neuron. It was possible to repeat this type of experiment (with the monkey stationary) for 20 of the 40 cells analysed. In all 20 cases, the cells responded when the monkey was stationary but looking at and visually exploring the environment. In all 20 cases, it was shown, as in Figure 2, that the cells could respond when the monkey was in different places in the environment, and that the critical factor in determining the firing rate of the cell was where in the environment the monkey was looking. The spatial view fields measured when the monkey was exploring the spatial environment using eye movements but with the head and body still were in all cases consistent with those measured during active locomotion.

The properties of each of the cells in the hippocampal formation analysed in this investigation are shown in Table 1. Because their firing rates depend on where the monkey is looking in space and not on the place where the monkey is currently located or on head direction, they are described as 'spatial view' cells and not as place cells. The spatial view fields varied in size from a small fraction of a wall (1/16th of its area) to an area equivalent to approximately a whole wall. The 20 cells in the hippocampal pyramidal cell fields CA3 or CA1 (Fig. 3) were probably hippocampal pyramidal cells, as shown by the large-amplitude action potentials, very low spontaneous firing rates (mean, 0.5 spikes/s) and relatively low peak firing rates (mean, 17 spikes/s; interquartile range, 11–20 spikes/s). Of the 20 in the overlying cortical areas, which connect the hippocampus to other cortical areas, 12 were in the parahippocampal gyrus and eight in the presubiculum. The mean spontaneous firing rate in the parahippocampal gyrus of the spatial view neurons was 0.6 spikes/s, and the peak firing rates had a mean of 15 spikes/s and an interquartile range of 11–19 spikes/s. The mean spontaneous firing rate of the presubicular spatial view neurons was 1 spike/s, and the peak firing rates had a mean of 11 spikes/s and an interquartile range of 7–15 spikes/s.

It was possible to repeat these types of experiment for 40 neurons from a sample of 352 recorded in two rhesus macaques. For all 40 spatial view cells it was possible to show that the major determinant of the cell's responses was where the monkey looked, not where the monkey was. All the cells had significant effects in one-way analysis of variance which tested whether the firing rate depended on where in the environment the monkey looked. All of the cells could fire when the monkey was at different places in the environment (provided that he looked at the appropriate part of the environment), and thus none was a place cell. (An example of a cell that could fire in different places is illustrated in Fig. 2). All of the spatial view cells could fire for different head directions (provided that the monkey looked at the appropriate part of the environment), and thus none was a head direction cell. Further evidence that they were not head direction cells is that we have recently discovered head direction cells in the monkey, and they are very different, displaying fine tuning for head direction even in different environments, and are found for example in the subicular complex rather than the hippocampus proper. (These cells are to be the subject of a separate publication). The spatial view cells active in this particular environment constituted ~11% of the cells analysed in this brain region. Among the other cells, as will be described in future reports, were not only head direction cells, but also egocentric cells (Feigenbaum and Rolls, 1991), and cells, probably interneurons, that increased their firing rate during locomotion.

Although some investigators describe place cells in rats as having some directionality (Markus *et al.*, 1995), in that they may respond when the rat is facing in one direction but not another, such cells in rats are clearly different from the cells described here, in that rat place cells only respond when the rat is in the place field. The cells described here are also different from the 'place' cells described by Ono *et al.* (1993) in the monkey, which require the monkey to be in a given place for a response to occur. The cells described here are also different from the object cells described by Rolls *et al.* (1989), Ono *et al.* (1993) and Eifuku *et al.* (1995), in that although every cell was tested none of the spatial view cells responded to objects placed in front of the monkey or depended on the monkey performing a particular task. In contrast, the cells described here responded when the monkey looked towards a view, independently of the place where the monkey is. The cells described here could be called place cells in that they respond to the place where the monkey is looking, not

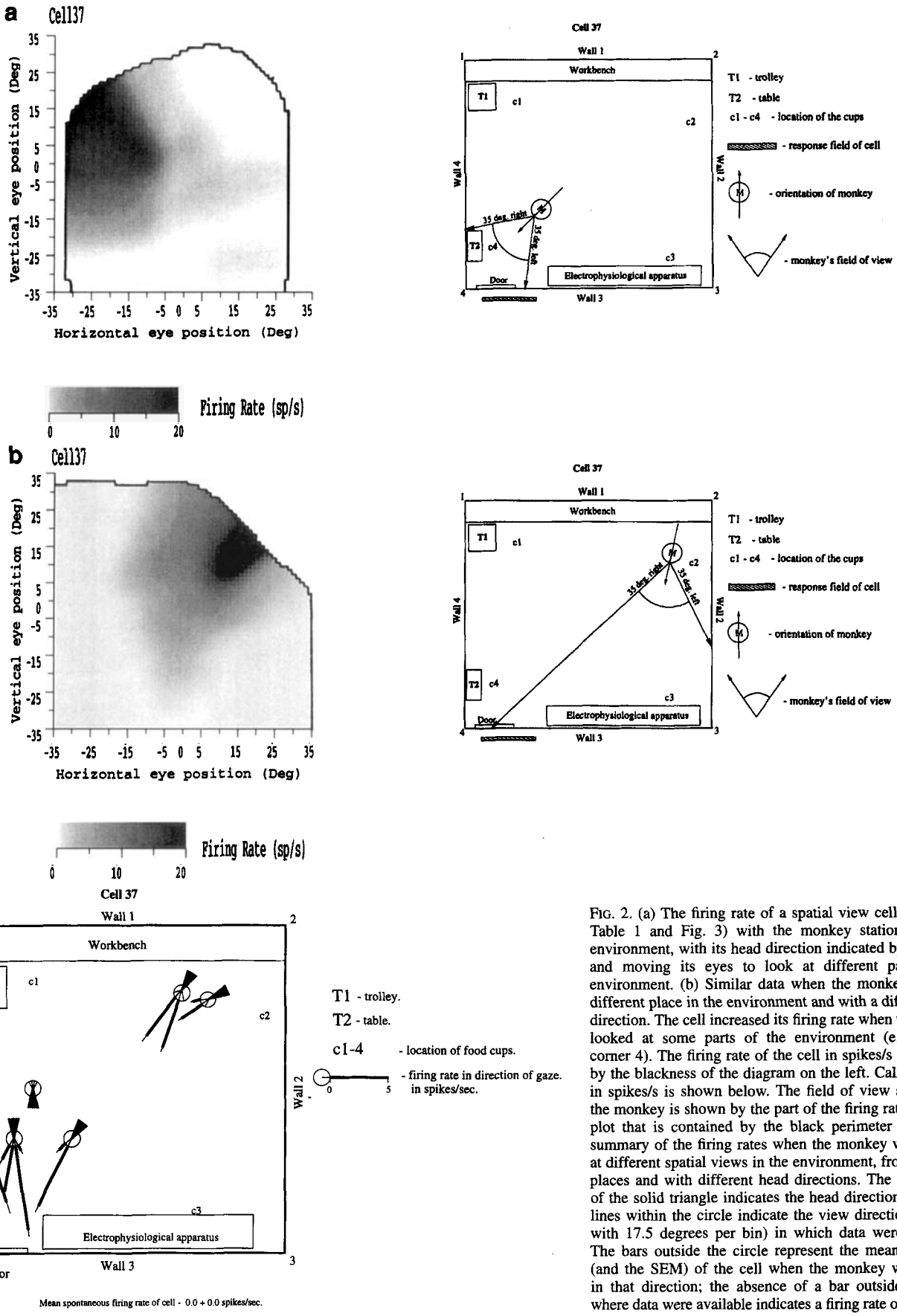

FIG. 2. (a) The firing rate of a spatial view cell (cell 37 in Table 1 and Fig. 3) with the monkey stationary in the environment, with its head direction indicated by the arrow and moving its eyes to look at different parts of the environment. (b) Similar data when the monkey was at a different place in the environment and with a different head direction. The cell increased its firing rate when the monkey looked at some parts of the environment (e.g. towards corner 4). The firing rate of the cell in spikes/s is indicated by the blackness of the diagram on the left. Calibration bar in spikes/s is shown below. The field of view sampled by the monkey is shown by the part of the firing rate greyscale plot that is contained by the black perimeter line. (c) A summary of the firing rates when the monkey was looking at different spatial views in the environment, from different places and with different head directions. The acute angle of the solid triangle indicates the head direction. The short lines within the circle indicate the view directions (binned with 17.5 degrees per bin) in which data were available. The bars outside the circle represent the mean firing rate (and the SEM) of the cell when the monkey was looking in that direction; the absence of a bar outside the circle where data were available indicates a firing rate of 0 spikes/s.

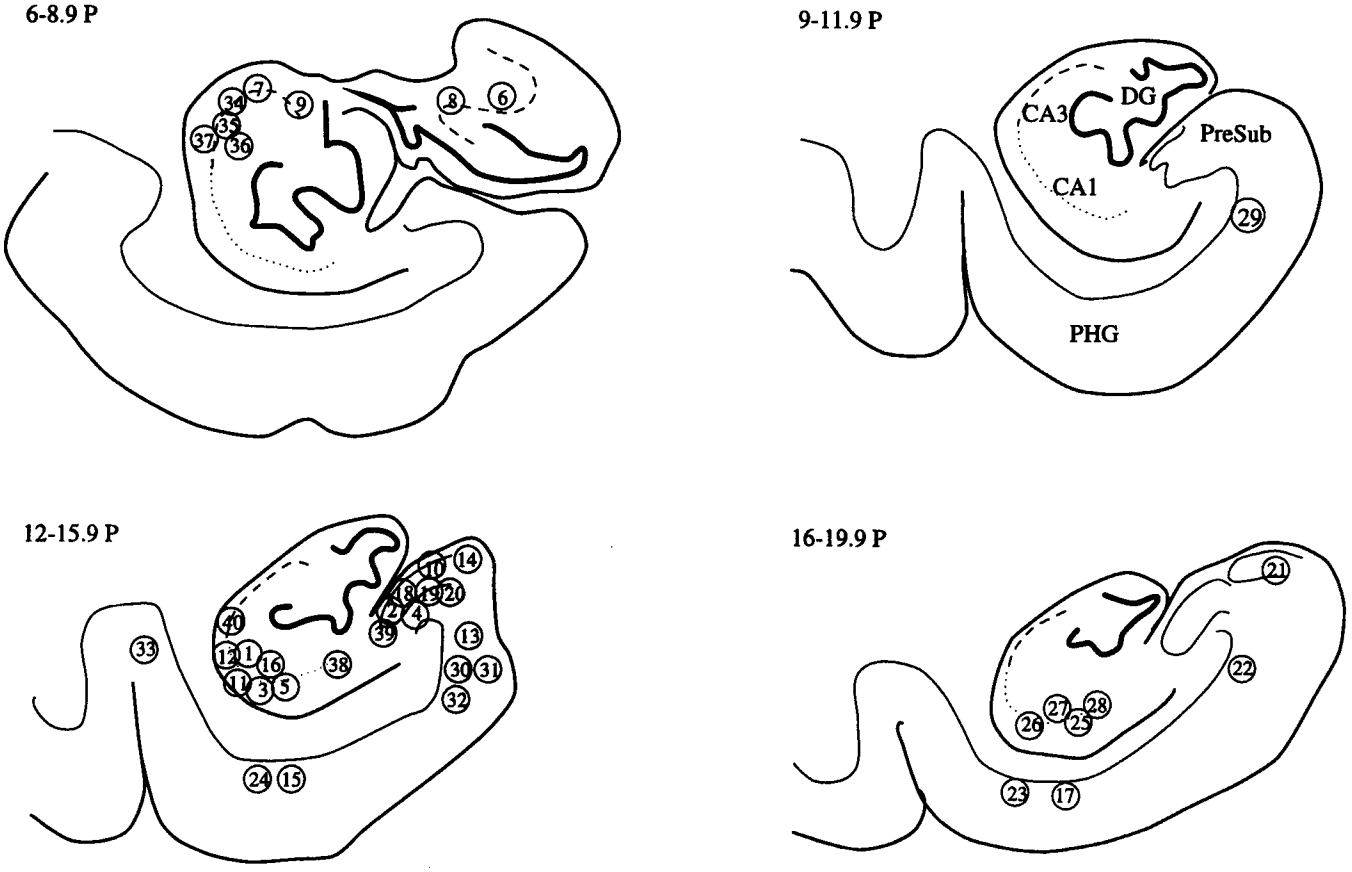

FIG. 3. The hippocampal and parahippocampal sites at which the different spatial view cells were recorded. The location of each is shown by a cell number, which corresponds to that used in Table 1. Coronal sections at different distances in millimetres posterior (P) to the sphenoid reference are shown. CA1, CA1 hippocampal pyramidal cell field; CA3, CA3 hippocampal pyramidal cell field; DG, dentate gyrus; PreSub, presubiculum; PHG, parahippocampal gyrus. Of the spatial view cells, 20 were hippocampal pyramidal cells (CA1 or CA3, 18% of those recorded in this region) and 20 were in the parahippocampal gyrus and presubiculum (14% of those recorded in these regions).

where he is. However, to distinguish the two types of cell we use the term 'spatial view cells' to describe the cells described here in monkeys. The issue of what is present at the spatial view that determines the response will be the subject of further investigation. However, it has already been shown, using ceiling-to-floor black curtains that fully obscured the sight of any particular objects, that the response of many cells can still continue (although the responses were typically less selective, see example in Fig. 1b, by comparison with Fig. 1a for the same cell). This is an indication that it is not the sight of a particular object but instead is knowledge of where the monkey is looking in space that is a condition for these neurons to respond. Further evidence that the actual sight of individual objects was not what activated these neurons was that moving individual objects out of a spatial view field did not abolish the responses of these neurons, and that the spatial view fields were often larger than any object (e.g. Fig. 1a). (For example, cells shown in Table 1 as responding when the monkey looked at the location of a particular cup also responded to the location when the cup was removed.) Further evidence consistent with the description of these neurons as spatial view neurons is that, as will be described in future reports, their responses are clearly different from other neurons in some of these regions that can be shown to respond to objects, and have such responses independently of where the object is in space.

Many 'spatial view' cells have thus been found in this series of experiments. No place cells have been found in this series of experiments that responded based on where the monkey was and not on where he was looking in the environment. These spatial view cells in the primate hippocampus are thus unlike place cells found in the rat (O'Keefe, 1979; Muller *et al.*, 1991; Burgess *et al.*, 1994). Primates, with their highly developed visual and eye movement control systems, can explore and remember information about what is present at places in the environment without having to visit those places. Such view cells in primates would thus be useful as part of a memory system, in that they would provide a representation of a part of space which would not depend on exactly where the monkey was, and which could be associated with items that might be present in those spatial locations. An example of the utility of such a representation in monkeys might be in enabling a monkey to remember where it had seen ripe fruit, or in humans of remembering where they had seen a person, or where they had left keys. We believe that the spatial representation described here in the primate hippocampus would be appropriate as the spatial representation used in the memory of particular events or episodes, in which the spatial component often provides an integral part, and in other cases provides part of the context for the memory (Rolls, 1996).

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