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Spatial View Cells and the Representation of Place in the Primate Hippocampus

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ABSTRACT: The information represented in the primate hippocampus is being analysed by making recordings in monkeys actively walking in the laboratory. In a sample of 352 cells recorded in this situation, no "place" cells have so far been found. Instead, we have found a considerable population of "spatial view" cells tuned to respond when the monkey looks at small parts of the environment. We have been able to demonstrate (1) that these hippocampal neurons respond to a view of space "out there," not to the place where the monkey is; (2) that the responses depend on where the monkey is looking, by measuring eye position; (3) that the responses in some cases (e.g., CA1 but not CA3) still occur if the view details are obscured with curtains; (4) that the cells (in, e.g., CA1) retain part of their "space" tuning even in complete darkness, for several minutes; and (5) that the spatial representation is allocentric. The spatial representation is, thus, different from that in the rat hippocampus, in which place cells respond based on where the rat is located. The representation is also different from that described in the parietal cortex, where neurons respond in egocentric coordinates. This representation of space "out there" provided by primate spatial view cells would be an appropriate part of a memory system involved in memories of particular events or episodes, for example, of where in an environment an object was seen. Spatial view cells (in conjunction with whole body motion cells in the primate hippocampus, and head direction cells in the primate presubiculum) would also be useful as part of a spatial navigation system, for which they would provide a memory component. *Hippocampus 1999;9:467–480.* © 1999 Wiley-Liss, Inc.

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The aims of this paper are to consider how space is represented in the primate hippocampus, how this is related to the memory and spatial functions performed by the hippocampus, and how the hippocampus performs these functions. The neurophysiological studies described have been performed (unless stated otherwise) with macaque monkeys in order to provide information as relevant as possible to understanding memory and spatial systems in humans. Given the great development of vision in primates relative to rodents, and with it the temporal cortical visual areas concerned with vision (which provide many inputs to the hippocampus via for example the perirhinal cortex), it is important to investigate whether hippocampal processing of space is identical to that of rats, in which place cells are found (McNaughton et al., 1983; O'Keefe, 1984; Muller et al., 1991; Markus et al., 1995).

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Because of the developments of the primate brain, some of the connections received by the primate hippocampus are reviewed, as they are relevant to understanding the types of neuron found in the primate hippocampus. The primate hippocampus receives inputs via the entorhinal cortex (area 28) and the highly developed parahippocampal gyrus (areas TF and TH) as well as the perirhinal cortex from many areas of the cerebral association cortex, including the visual and auditory temporal lobe association cortical areas, the prefrontal cortex, and the parietal cortex (Van Hoesen, 1982; Amaral, 1987; Suzuki and Amaral, 1994) (see Fig. 1). In addition, the entorhinal cortex receives inputs from the amygdala. There are also subcortical inputs from, for example, the amygdala and septum. The hippocampus, in turn, projects back via the subiculum, entorhinal cortex, and parahippocampal gyrus (area TF-TH), to the cerebral cortical areas from which it receives inputs (Van Hoesen, 1982), as well as to subcortical areas such as the mammillary bodies (see Fig. 1).

In the studies of neuronal responses in the primate hippocampus that will be described, the recordings of neuronal activity have generally been made while the hippocampus is performing the functions for which lesion studies have shown it is needed. Lesion studies have shown that damage to the hippocampus or to some of its connections, such as the fornix in monkeys, produces deficits in learning about the places of objects and about the places where responses should be made. For example, macaques and humans with damage to the hippocampus or fornix are impaired in object-place memory tasks in which not only the objects seen, but where they were seen, must be remembered (Smith and Milner, 1981; Gaffan and Saunders, 1985; Parkinson et al., 1988). Such object-place tasks require a whole scene or snapshot-like memory in which spatial relations in a scene must be remembered (Gaffan, 1994). Also, fornix lesions impair conditional left-right discrimination learning, in which the visual appearance of an object specifies whether a response is to be made to the left or the right (Rupniak and Gaffan, 1987). A comparable deficit is found in humans (Petrides, 1985). Fornix-sectioned monkeys are also impaired in learning on the basis of a spatial cue which object to choose (e.g., if two objects are

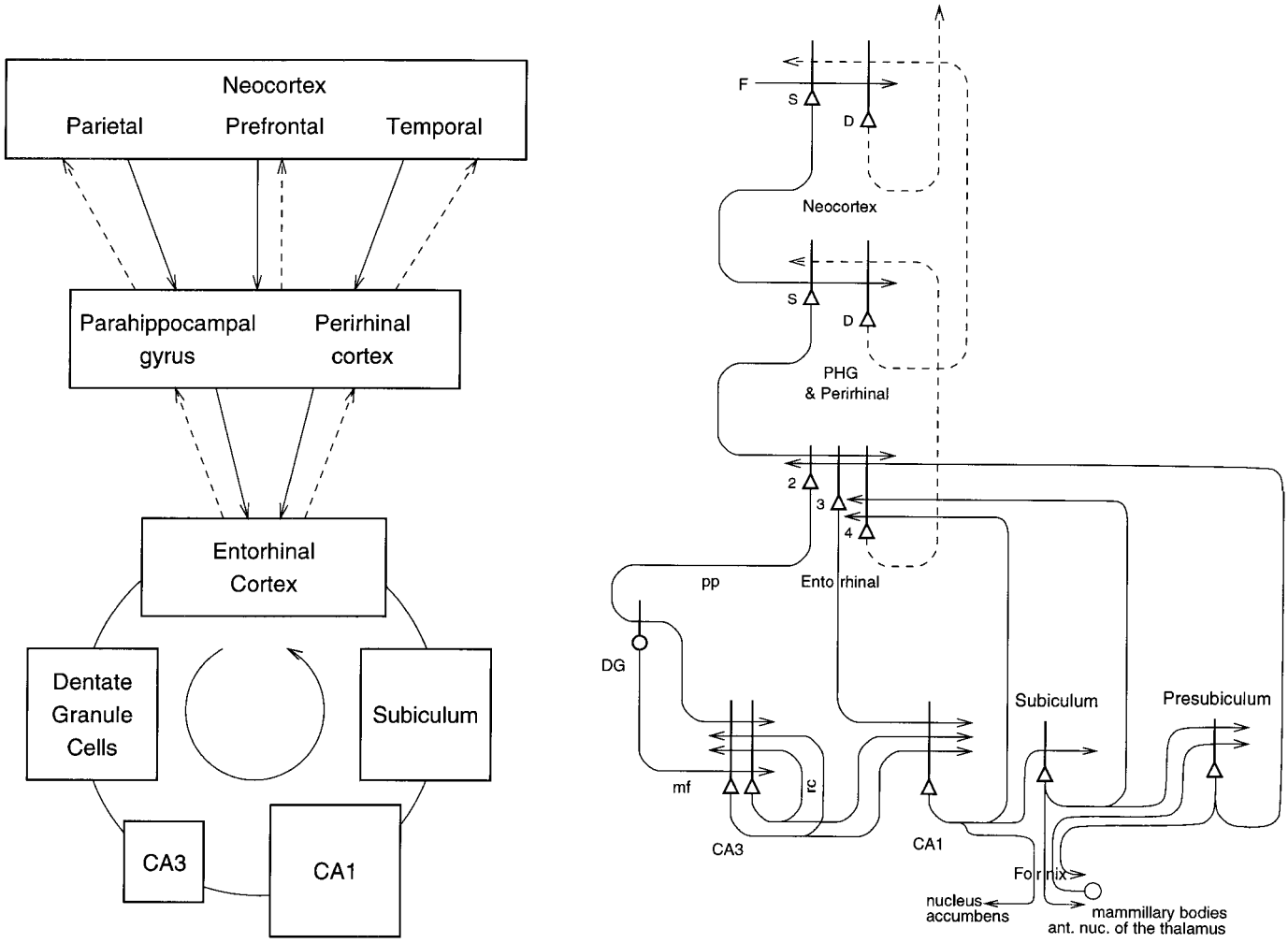

FIGURE 1. Forward connections (solid lines) from areas of cerebral association neocortex via the parahippocampal gyrus and perirhinal cortex, and entorhinal cortex, to the hippocampus; and backprojections (dashed lines) via the hippocampal CA1 pyramidal cells, subiculum, and parahippocampal gyrus to the neocortex. There is great convergence in the forward connections down to the single network implemented in the CA3 pyramidal cells; and great divergence again in the backprojections. Left: Block diagram. Right: More detailed representation of some of the principal excitatory neurons in the pathways. D: deep pyramidal cells; DG: dentate granule cells; F: forward inputs to areas of the association cortex from preceding cortical areas in the hierarchy; mf: mossy fibres; PHG: parahippocampal gyrus and perirhinal cortex; pp: perforant path; rc: recurrent collateral of the CA3 hippocampal pyramidal cells; S: superficial pyramidal cells; 2: pyramidal cells in layer 2 of the entorhinal cortex; 3: pyramidal cells in layer 3 of the entorhinal cortex. The thick lines above the cell bodies represent the dendrites.

on the left, choose object A, but if the two objects are on the right, choose object B) (Gaffan and Harrison, 1989a). Monkeys with fornix damage are also impaired in using information about their place in an environment. For example, Gaffan and Harrison (1989b) found learning impairments when which of two or more objects the monkey had to choose depended on the position of the monkey in the room.

In recordings made in the primate hippocampus under similar conditions to those in which place cells would be found in rats, we have not so far found neurons that respond in relation to the place where the monkey is. Instead, we have found spatial view cells, which may be thought of as responding to the place at which the monkey is looking. Because these neurons are in some sense concerned with place, their properties are described in this paper. The way in which these cells were discovered, and some of the tasks in which they respond, are as follows.

Memory for the Positions of Responses and for the Places of Stimuli in Memory Tasks

Watanabe and Niki (1985) analysed hippocampal neuronal activity while monkeys performed a delayed spatial response task. In a delayed spatial response task, a stimulus is shown on, for example, the left, there is then a delay period, and after this the monkey can respond, for example, by touching the left stimulus position. They reported that 6.4% of hippocampal neurons responded differently while the monkey was remembering left as compared to right. The responses of these neurons could reflect

preparation for the spatial response to be made, or they could reflect memory of the spatial position in which the stimulus was shown. To provide evidence on which was important, Cahusac et al. (1989) analysed hippocampal activity in this task, and in an object-place memory task. In the object-place memory task, the monkey was shown a sample stimulus in one position on a video screen, there was a delay of 2 s, and then the same or a different stimulus was shown in the same or in a different position. The monkey remembered the sample and its position, and if both matched the delayed stimulus, he licked to obtain fruit juice. Of the 600 neurons analysed in this task, 3.8% responded differently for the different spatial positions, with some of these responding differentially during the sample presentation, some in the delay period, and some in the match period. Thus, some hippocampal neurons (those differentially active in the sample or match periods) respond differently for stimuli shown in different positions in space, and some (those differentially active in the delay period) respond differently when the monkey is remembering different positions in space. In addition, some of the neurons responded to a combination of object and place information, in that they responded only to a novel object in a particular place. These neuronal responses were not due to any response being made or prepared by the monkey, because information about which behavioral response was required was not available until the match stimulus was shown. Cahusac et al. (1989) also found that the majority of the neurons that responded in the object-place memory task did not respond in the delayed spatial response task. Instead, a different population of neurons (5.7% of the total) responded in the delayed spatial response task, with differential left-right responses in the sample, delay, or match periods. Thus, this latter population of hippocampal neurons had activity that was related to the preparation for or initiation of a spatial response, which in the delayed response task could be encoded as soon as the sample stimulus was seen.

These recordings showed that there are some neurons in the primate hippocampus with activity that is related to the spatial position of stimuli or to the memory of the spatial position of stimuli (as shown in the object-place memory task). The recordings also showed that information about which visual stimulus was shown, and where it was shown, was combined onto some neurons in the primate hippocampus.

Object-Place Memory Tasks

The responses of hippocampal neurons in primates with activity related to the place in which a stimulus is shown were further investigated using a serial multiple object-place memory task. The task required a memory for the position on a video monitor in which a given object had appeared previously (Rolls et al., 1989). This task was designed to allow a wider area of space to be tested than in the previous study, and was chosen also because memory of where objects had been seen previously in space was known to be disrupted by hippocampal damage (Gaffan and Saunders, 1985; Gaffan, 1987). In the task, a visual image appeared in one of 4 or 9 positions on a screen. If the stimulus had been seen in that position before, the monkey could lick to obtain fruit juice, but if the image had not appeared in that position before, the monkey had not to lick in order to avoid the taste of saline. Each image appeared in each position on the screen only twice, once as novel, and once as familiar. The task thus required memory not only of which visual stimuli had been seen before, but of the positions in which they had been seen, and is an object-place memory task. It was found that 9% of neurons recorded in the hippocampus and parahippocampal gyrus had spatial fields in this and related tasks, in that they responded whenever there was a stimulus in some but not in other positions on the screen. In total, 2.4% of the neurons responded to a combination of spatial information and information about the object seen, in that they responded more the first time a particular image was seen in any position. Six of these neurons were found, which showed this combination even more clearly, in that they responded only to some positions, and only provided that it was the first time that a particular stimulus had appeared there. Thus, not only is spatial information processed by the primate hippocampus, but it can be combined as shown by the responses of single neurons with information about which stimuli have been seen before (Rolls et al., 1989).

The ability of the hippocampus to form such arbitrary associations of information that may from the parietal cortex about position in space with information originating from the temporal lobe about objects may be important for its role in memory. Moreover, these findings provide neurophysiological support for the computational theory according to which arbitrary associations should be formed onto single neurons in the hippocampus between signals originating in different parts of the cerebral cortex, e.g., about objects and about position in space (see Treves and Rolls, 1994; Rolls, 1996a; Rolls and Treves, 1998).

Allocentric Representation of Space in the Primate Hippocampus

These studies showed that some hippocampal neurons in primates have spatial fields. In order to investigate how space is represented in the hippocampus, Feigenbaum and Rolls (1991) investigated whether the spatial fields use egocentric or some form of allocentric coordinates. This was investigated by finding a neuron with a space field, and then moving the monitor screen and the monkey relative to each other, and to different positions in the laboratory. For 10% of the spatial neurons, the responses remained in the same position relative to the monkey's body axis when the screen was moved or the monkey was rotated or moved to a different position in the laboratory. These neurons, thus, represented space in egocentric coordinates. For 46% of the spatial neurons analysed, the responses remained in the same position on the screen or in the room when the monkey was rotated or moved to a different position in the laboratory. These neurons, thus, represented space in allocentric coordinates. Evidence for two types of allocentric encoding was found. In the first type, the field was defined by its position on the monitor screen independently of the position of the monitor relative to the monkey's body axis and independently of the position of the monkey and the screen in the laboratory. These neurons were

called "frame of reference" allocentric, in that their fields were defined by the local frame provided by the monitor screen. The majority of the allocentric neurons responded in this way. In the second type of allocentric encoding, the field was defined by its position in the room, at which the monkey was looking, and was relatively independent of position relative to the monkey's body axis or to position on the monitor screen face. These neurons were called "absolute" allocentric, in that their fields were defined by position in the room. They are what we have gone on to show subsequently are spatial view neurons. These results showed that in addition to neurons with egocentric spatial fields, which have also been found in other parts of the brain such as the parietal cortex (Andersen, 1995), there are neurons in the primate hippocampal formation that encode space in allocentric coordinates.

Spatial View Neurons in the Primate Hippocampus

In rats, place cells are found that respond depending on the place where the rat is in a spatial environment (see McNaughton et al., 1983; O'Keefe, 1984; Muller et al., 1991). In a first investigation to analyse whether such cells might be present in the primate hippocampus, Rolls and O'Mara (1993, 1995) recorded the responses of hippocampal cells when macaques were moved in a small chair or robot on wheels in a cue-controlled testing environment (a $2 \times 2 \times 2$ m chamber with matt black internal walls and floors). Tests were performed to determine whether cells might be found that could be described as "place-related," i.e., firing differently when macaques are moved to different places in this environment; or according to the position in space at which the monkey is looking; or according to his "head direction." The most common type of cell responded to the part of space at which the monkeys were looking, independently of the place where the monkey was. These neurons were called "view" neurons, and are similar to the space neurons described by Rolls et al. (1989), and Feigenbaum and Rolls (1991). [The main difference was that in the study of Rolls et al. (1989) and Feigenbaum and Rolls (1991), the allocentric representation was defined by where on a video monitor a stimulus was shown; whereas spatial view cells respond when the monkey looks at a particular part of a spatial environment.] Some of these view neurons had responses that depended on the proximity of the monkey to what was being viewed. Thus, in this study the neuronal representation of space found in the primate hippocampus was shown to be defined primarily by the view of the environment, and not by the place where the monkey was (Rolls and O'Mara, 1993, 1995). Ono et al. (1993) performed studies on the representation of space in the primate hippocampus while the monkey was moved in a cab to different places in a room. They found that 13.4% of hippocampal formation neurons fired more when the monkey was at some than when at other places in the test area, and although some neurons responded more when the monkey was at some places than at others, it was not clear whether the responses of these neurons responded to the place where the monkey was independently of spatial view, or whether the responses of place-like cells were view dependent. This critical issue is discussed after the properties of spatial view cells have been described further, when tests that can distinguish spatial view cells from place cells will become more clear.

In rats, place cells fire best during active locomotion by the rat (Foster et al., 1989). To investigate whether place cells might be present in monkeys if active locomotion was being performed, in current experiments we (Rolls et al., 1997a, 1998; Robertson et al., 1998; Georges-François et al., 1999) recorded from single hippocampal neurons while monkeys move themselves round the test environment by walking. Also, to bring out the responses of spatial cells in the primate hippocampus, we changed from the cue-controlled environment of Rolls and O'Mara (1995), which was matt black apart from four spatial cues, to the much richer environment of the open laboratory, within which the monkey has a 2.5×2.5 m area to walk. The position and head direction of the monkey are tracked continuously, and the eye position (i.e., the horizontal and vertical directions of the eyes with respect to the head) is recorded continuously with the scleral search coil technique so that we can measure exactly where the monkey is looking in the environment at all times. An example of a hippocampal pyramidal cell recorded during active locomotion in this environment is shown in Figure 2. Figure 2a shows in the outer set of rectangles all the firing that occurred during a period of 6 min when the monkey was walking around the laboratory. The icons of the cart position printed every 250 ms show that a wide area of the laboratory was explored during the period. The cell fired mainly when the monkey was looking at a part of wall 3, and this is brought out in Figure 2b and c in which a spot is placed on the walls where the monkey was looking only when the firing rate was above 12 spikes/s, the half-maximal firing rate. The fact that the cell responded when the monkey was looking at the spatial view field on wall 3 from a large number of different places in the room is shown in Figure 2b, in which every 10th cart position and horizontal gaze direction when the cell fired at greater than 12 spikes/s is shown. The range of different cart positions and head directions (which were aligned with the cart direction) over which the cell fired when the cell responded at more than 12 spikes/s is illustrated in Figure 2c, in which every cart position and head direction for this response rate is shown. Further analyses of the response properties of this cell, including evidence that it responded for a whole set of different head positions, head directions, and eye positions, and that it had similar spatial view fields when the monkey was actively walking and when he was stationary but exploring the environment with eye movements, are provided by Georges-François et al. (1999).

The responses of another cell to show how the responses are related to spatial view, and not to place, head direction, or eye position per se are shown in Figure 3. The firing of the cell as a function of horizontal and vertical eye position is shown in Figure 3a (left) with the monkey stationary at the place and with the head direction shown in Figure 3a (right). (The firing rate of the neuron was measured whenever the eyes were stationary to within 1° for more than 250 ms, and data for several minutes of recording are shown.) The highest firing rate of the cell was found when the monkey was looking approximately 10° left and level in the

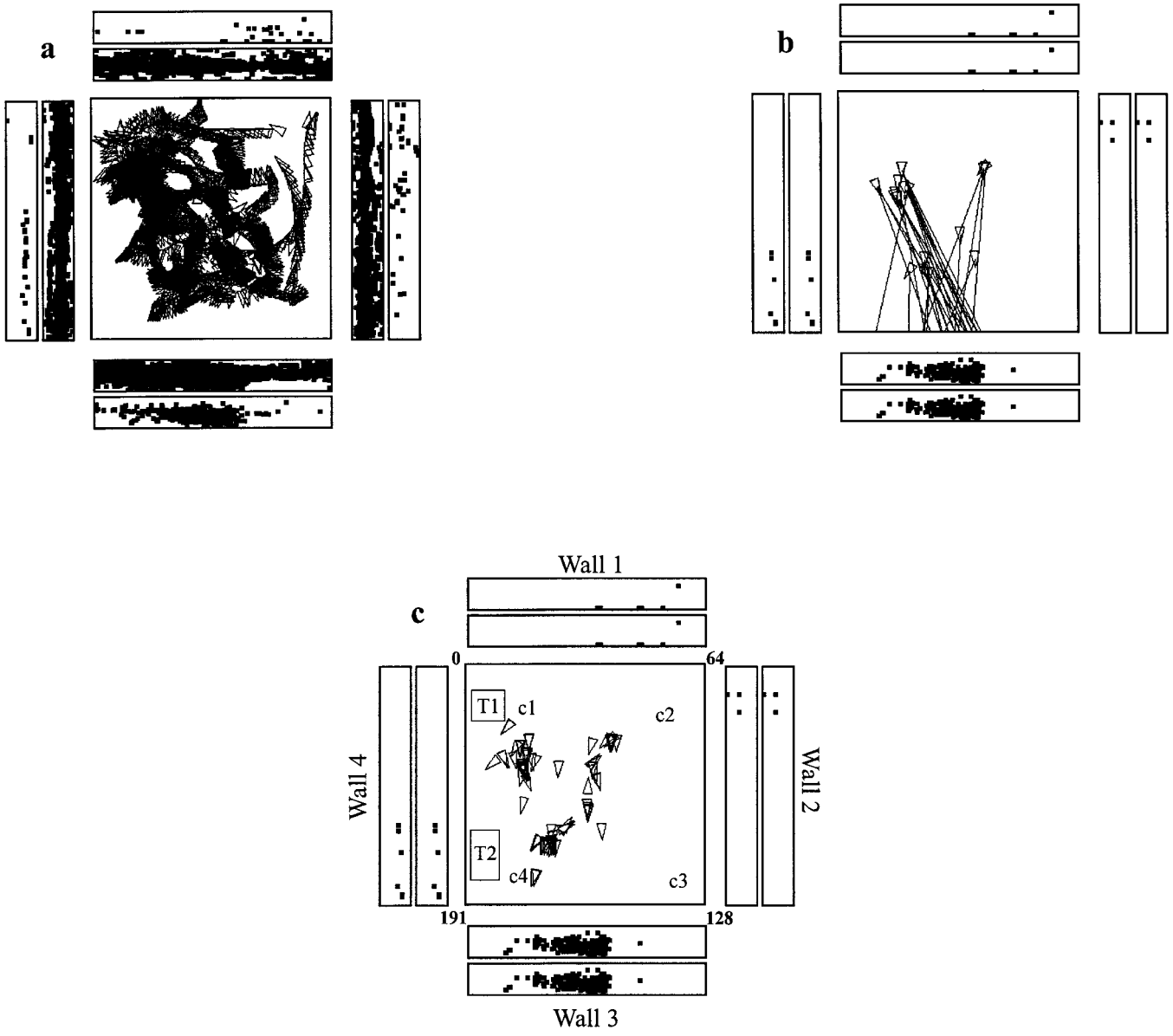

FIGURE 2. Examples of the firing of a hippocampal cell (az033) when the monkey was walking around the laboratory. a: The firing of the cell is indicated by the spots in the outer set of 4 rectangles, each of which represents one of the walls of the room. There is one spot on the outer rectangle for each action potential. The base of the wall is towards the centre of each rectangle. The positions on the walls fixated during the recording sessions are indicated by points in the inner set of 4 rectangles, each of which also represents a wall of the room. The central square is a plan view of the room, with a triangle printed every 250 ms to indicate the position of the cart, thus showing that many different places were visited during the recording sessions. b: A similar representation of the same 3 recording sessions as in a, but modified to indicate some of the range of cart positions and horizontal gaze directions when the cell fired. Sufficiently few cart/eye gaze direction icons so that they can be distinguished were selected by plotting only every 10th icon when the cell fired faster than 12 spikes/s. A spot was placed in the rectangles whenever the cell fired at greater than 12 spikes/s. c: A similar representation of the same 3 recording sessions as in b, but modified to indicate more fully the range of cart positions when the cell fired. Sufficiently few cart icons so that they can be distinguished were selected by plotting every cart icon when the cell fired faster than 12 spikes/s. (12 spikes/s was selected as it was half the peak firing rate of the cell, and thus helps to reveal the conditions when the cell was strongly activated.) The triangle indicates the current position of the monkey, and the line projected from it shows which part of the wall is being viewed at any one time while the monkey is walking. One spot is shown for each action potential. (Reproduced with permission from Georges-Francois et al. [1999] and Oxford University Press; Cerebral Cortex 9:197–212, 1999.)

vertical plane. The response field of the cell is plotted against wall 1 in Figure 3a (right). The recording time for the data shown in Figure 3a was approximately 4 min. The monkey was then moved to the different place with a different head direction shown in Figure 3b. The highest firing rate was now when the monkey was looking approximately 30° right. The response field of the cell is again plotted against wall 1 in Figure 3b (right). Data with the monkey at a different place (but the same head direction as in Fig.

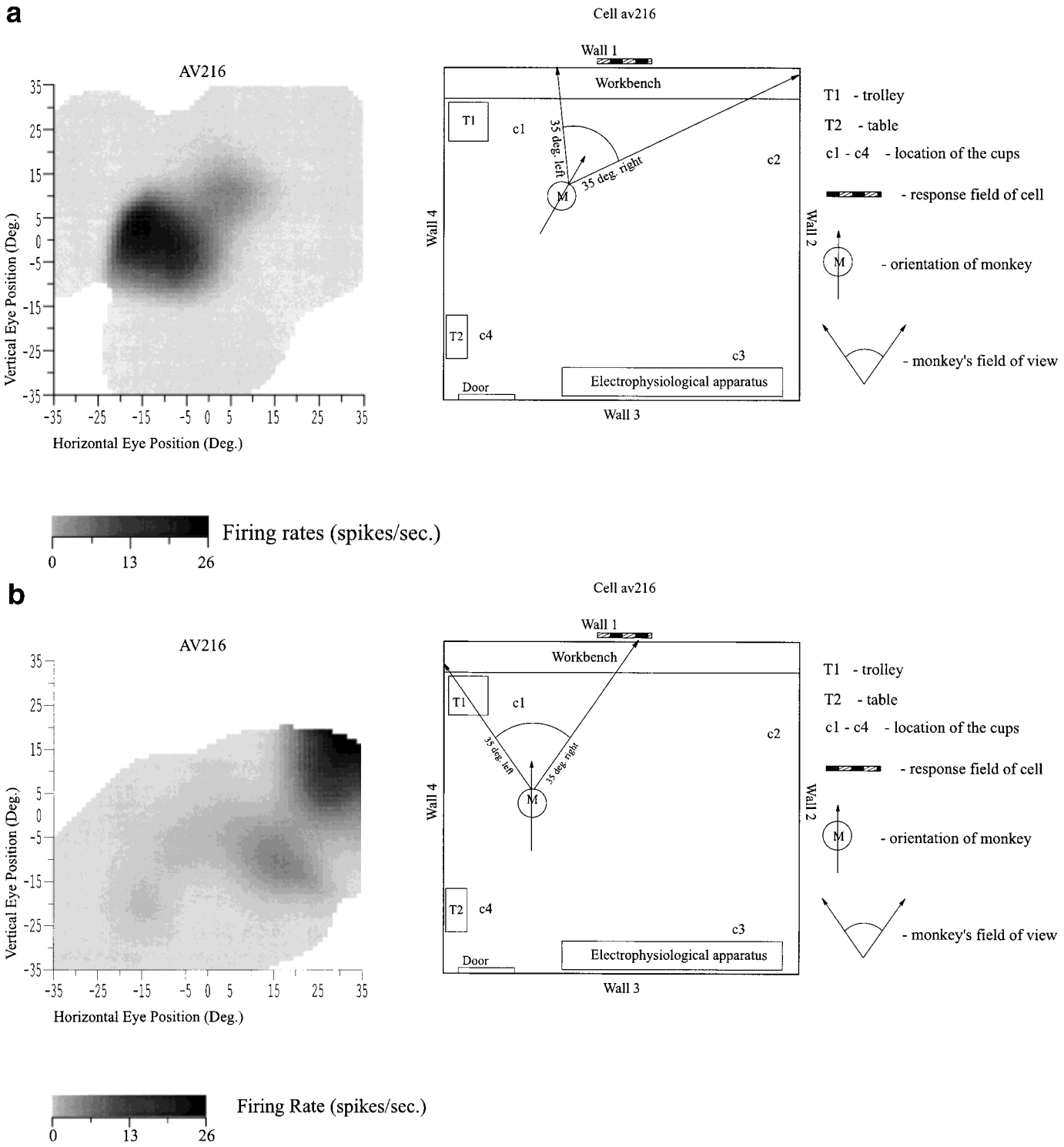

FIGURE 3. Examples of the firing of another hippocampal cell (av216) when the monkey was at different positions in the room, with different head directions, looking at wall 1 of the room. The details of the spatial view field are shown by the different firing rates indicated as gray scale levels. The firing rate of the cell in spikes/s as a function of horizontal and vertical eye position is indicated by the blackness of the diagram on the left (with the calibration bar in spikes/s shown below). (Positive values of eye position represent right in the horizontal plane and up in the vertical plane.) The hatched box in the diagram on the right represents the approximate position of the spatial view field. a–c: Experiments with the monkey in different places, and with different head directions. (Reproduced with permission from Georges-Francois et al. [1999] and Oxford University Press; Cerebral Cortex 9:197–212, 1999.)

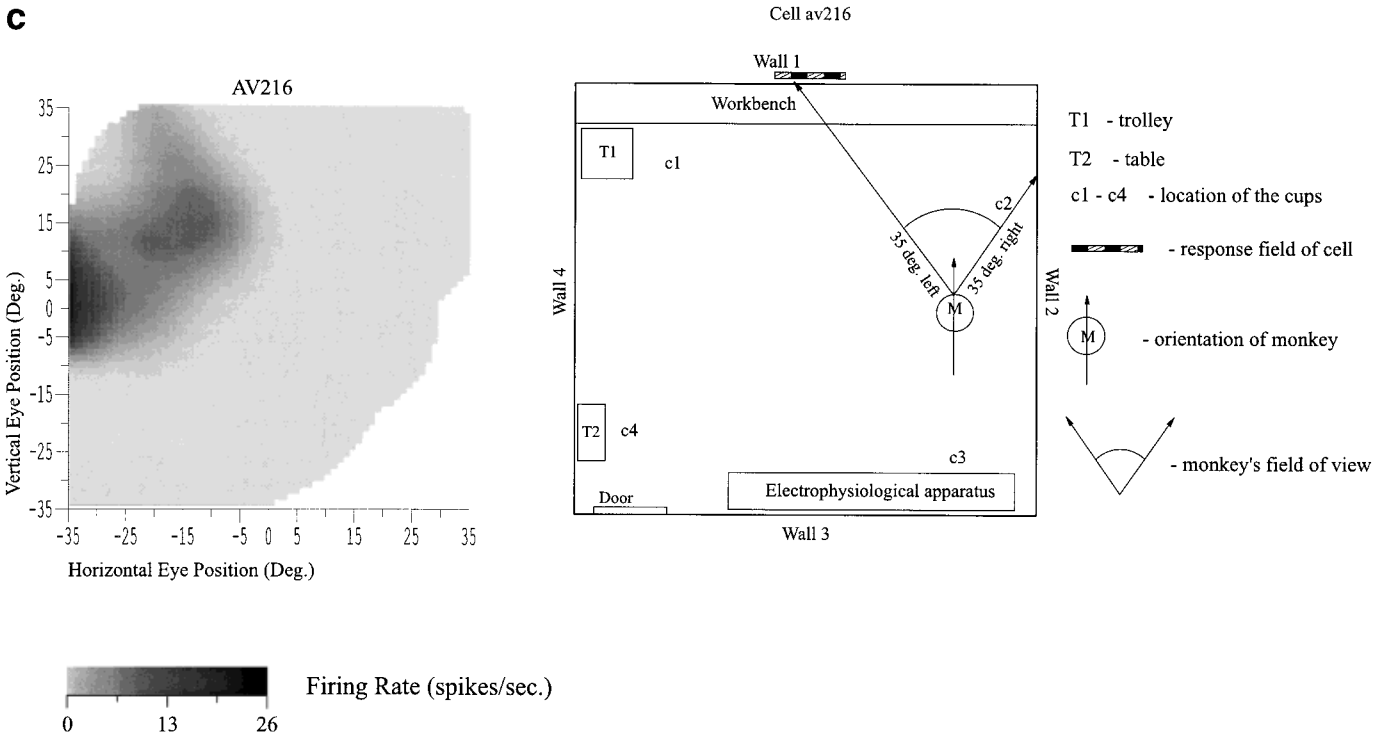

FIGURE 3. (Continued).

3b) are shown in Figure 3c. The cell now fired most when the monkey looked approximately 30° left. The response field was, however, at the same place on Wall 1 as in Figure 3a and b. It is clear from this type of experiment that it was where the monkey was looking that determined whether the neuron responded, and not a particular head direction, eye position, or place where the monkey was located. This was confirmed in one-way analyses of variance, in which the several hundred firing rate and eye position data pairs used to construct Figure 3a–c were sorted according to different hypotheses. When the data for level eye position plus and minus 7° (the level of gaze where the cell fired if it was going to) were sorted according to where the monkey was looking on the wall (binned into 6 wall positions visible in Figure 3a–c), the one-way ANOVA was significant at $P < 0.001$ ($F(1,5) = 4.66$, and the cell provided an average information (about spatial view) of 0.217 bits in a 500-ms epoch. When the same data were sorted according to eye position (binned into 6 bins), the one-way ANOVA was not significant ($P \approx 0.8$, $F(1,3) = 0.35$), and the cell provided an average information (about eye position) of 0.006 bits in a 500-ms epoch. When the same data were sorted according to head direction (binned into 2 bins), the one-way ANOVA was not significant ($P \approx 0.5$, $F(1,1) = 0.45$), and the cell provided an average information (about head direction) of 0.0 bits in a 500-ms epoch. When the same data were sorted according to the place where the monkey was located (binned into 2 bins), the one-way ANOVA was not significant ($P \approx 0.9$, $F(1,1) = 0.02$), and the cell provided an average information (about place) of 0.001 bits in a 500-ms epoch. This analysis leads to the conclusion that the cell responded significantly differently for different allocentric spatial views and had information about spatial view in its firing rate, but did not respond differently just on the basis of eye position, head direction, or place. Across the population of cells analysed, it was possible to confirm that it was where the monkey was looking, and not the eye position, head direction, or head position in the room per se, which accounts for the firing of these neurons, and about which they convey most information (Georges-François et al., 1999). This series of experiments proved that the representation was not in egocentric spatial coordinates (with respect to the head or body), but was instead allocentric, representing positions in space in world-based coordinates.

In further experiments on these spatial view neurons, it was shown that the responses of some reflected quite an abstract representation of space, in that if the visual details of the view were completely obscured by floor-to-ceiling black curtains, then many of the neurons could still respond when the monkey looked towards where the view had been (Robertson et al., 1998). An example of such an experiment performed during active locomotion is shown in Figure 4. The inner set of four rectangular boxes show where the monkey looked on the four walls. (The top of each wall is furthest from the centre.) The outer set of 4 boxes again represent the 4 walls, but in these, a spot indicates where the cell fired. It is clear with the curtains drawn open that the cell has a spatial view field on wall 3 (Fig. 4a). The firing of the cell when the monkey moved round in the environment with the curtains closed is shown in Figure 4b. It is clear that with the curtains closed, the cell responded when the monkey looked at wall 3, that is the spatial selectivity of the cell was retained.

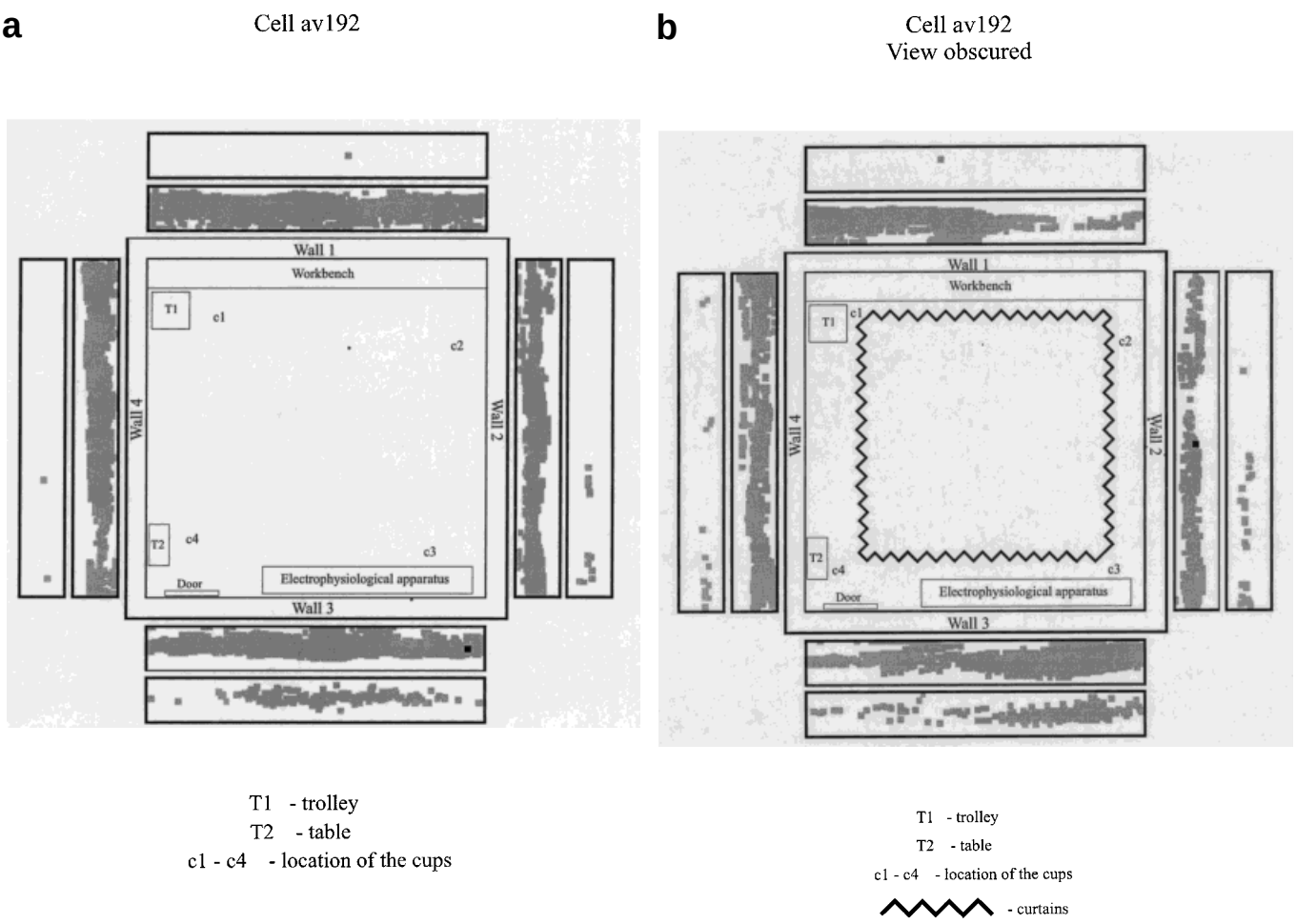

FIGURE 4. The firing rate of hippocampal formation cell av192 when the monkey was walking round in the environment. The inner set of four rectangular boxes is provided to show that the monkey looked during the experiment at all four walls of the environment. Each time he looked at a part of a wall for 0.25 s or more, a spot was placed at the location on the wall. (The top of each wall is furthest from the centre.) The outer set of 4 boxes again represent the four walls, but in these a spot indicates where the cell fired. a: The firing with the curtains drawn open, so that the room was visible. b: The firing of the cell when the monkey moved round in the environment with the curtains closed. The curtains are indicated by the zig-zag lines. (Adapted from Robertson et al., 1998, fig. 3).

Another example of a similar experiment, but with the monkey stationary thus allowing the firing to be shown on a diagram as a function of eye position, is shown in Figure 5. When the monkey was positioned in one place in the environment (with his feet touching a floor of his walker, not the lab floor), the firing rate of the cell was measured when the monkey looked at different parts of the environment (using the search coil to show where he was looking) in the light, with the curtains drawn open to show the full details of the view (Fig. 5a). Then the recording of neuronal activity and eye position were repeated with the curtains drawn closed to obscure all details of the view (Fig. 5b). When all the walls of the room were completely obscured by drawing the curtains, the neuron still responded whenever the monkey looked to approximately the same position in the room (Fig. 5b). (There was a slight drift of the view field when the curtains were closed, consistent with the hypothesis that a remembered spatial view is not as accurately located as a seen one, and with the fact that the actual view of the scene was the normal determinant of the spatial response field of the cell. The slight drift of the spatial field of the cell is also consistent with the evidence from the study reported by Georges-François et al., 1999, that the coordinate system used by these cells is not in eye position coordinates, nor in a combination of eye position and head direction coordinates, but in allocentric, i.e., world coordinates.) The experiment (Robertson et al., 1998; see also Rolls et al., 1997) shows that primate hippocampal spatial view neurons can be updated for at least short periods by idiothetic cues including eye position and head direction signals, and that the drift produced by the necessary temporal integration of these signals can then be corrected by showing the visual scene again.

The cells that responded with only a small diminution of their response when the view details were obscured (or the room was placed into darkness) were found in the CA1 region, the parahippocampal gyrus, and the presubiculum. Other cells had a large diminution (to on average 23% of their normal response) when the monkey looked towards the normally effective location

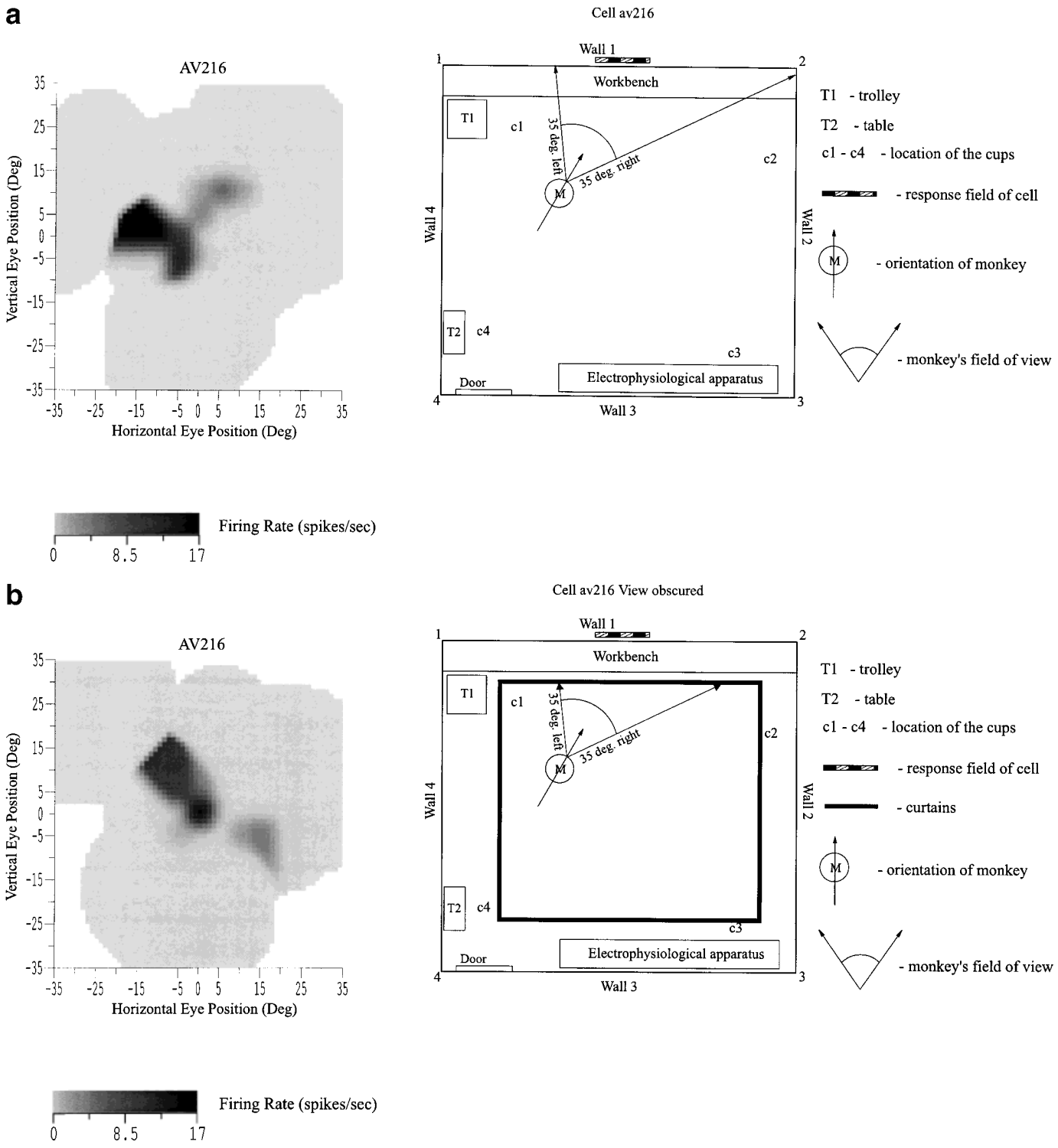

FIGURE 5. Example of the firing of a hippocampal formation cell (av216) with the monkey stationary with his head facing in the direction indicated by the arrow when the curtains were drawn open (a), or were drawn closed (b). The firing rate of the cell in spikes/s is indicated by the blackness of the diagram on the left (with the calibration bar in spikes/s shown below) projected onto the monkey's field of view. The 2D firing rate profile of the cell was smoothed for clarity using a 2D Gaussian spatial filter with a standard deviation of 0.2 of a pixel in a 14 × 14 array into which the firing rates were binned. (This degree of spatial smoothing is used to display the spatial view fields unless otherwise stated.) The space adequately sampled by the eye movements of the monkey is enclosed within a black perimeter. A plan view of the room to indicate the monkey's view of the wall is shown on the right. M indicates the position of the monkey. (Adapted from Robertson et al., 1998, fig. 2).

in the environment when the view details were obscured. These cells were in the CA3 region of the hippocampus. This finding provides additional evidence that visual inputs are important in defining the response properties of spatial view neurons (Robertson et al., 1998). This reduction in the firing of the CA3 cells reflects the reduction in the visual sensory drive or recall cue to a CA3 memory system. The results indicate that for CA3 cells, the visual input is necessary for the normal spatial response of the neurons, and for other cells in the primate hippocampal formation, the response still depends on the monkey gazing towards that location in space, when the view details are obscured (Robertson et al., 1998). These latter cells could, therefore, reflect the operation of a memory system, in which the neuronal activity can be triggered by factors that probably include not only (idiothetic) eye position command/feedback signals, but also probably vestibular and/or proprioceptive inputs. The fact that the CA3 neurons continue to fire in the dark and with the view obscured is evidence that there is an attractor (autoassociation) network implemented in the CA3 recurrent collateral system that can be triggered into an attractor state by the appropriate idiothetic signals (Rolls, 1989a,b, 1996a; Treves and Rolls, 1994; Rolls and Treves, 1998). The findings are consistent with partial recovery of information in the CA3 network, which may operate by autoassociation, and further recovery of information in the CA3 to CA1 associatively modifiable synapses, as has been shown to be possible in simulations and analytically (see Rolls, 1995, who demonstrated this retrieval effect of the Schaffer collaterals in simulations of the hippocampus, and Schultz and Rolls, 1999, who produced a quantitative analysis of this effect). Another factor that could contribute to the better responses of CA1 cells when the spatial view is obscured is the direct perforant path input to the CA1 cells, which may provide additional input to the CA1 cells (see Rolls and Treves, 1998).

The spatial view field of these cells typically occupies a part of space that is about as large as 1/16 to all of one of the walls of the testing room. Each cell has a different view to which it responds. Thus, over a population of many such neurons these partly overlapping view fields represent rather precise information about the part of space being viewed. This has been quantified using information theory, and indeed it has been shown that the amount of information about which part of space the monkey is viewing increases approximately linearly with the number of neurons in the sample. Thus, an independent contribution is made by each of the cells in an ensemble to representing allocentric space (Rolls et al., 1998). Because information is a logarithmic measure, this means that the number of spatial views (or the accuracy of the representation) increase exponentially with the number of neurons in the ensemble, a powerful result. Moreover, the present indication is that most of this information is contained in the number of spikes that each neuron produces within a short time window, and not in the relative time of firing of the spikes of different neurons (Panzeri et al., 1999).

Many spatial view (or "space" or "view") cells have been found in this series of experiments (Rolls et al., 1997a, 1998; Robertson et al., 1998; Georges-François et al., 1999). (The number of spatial view cells in the initial sample of 352 cells recorded under these conditions is 40, see Rolls et al., 1997a. It is simply noted here that their average spontaneous rate is low, mean 0.5 spikes/s, and that their average peak firing rate is 17 spikes/s, interquartile range 11–20 spikes/s. This low spontaneous rate and low peak response rate is similar to that of place cells in rats.) No place cells have been found that responded based on where the monkey was, and not on where he was looking in the environment. Although Ono et al. (1993) (see also Matsumura et al., 1999) have described cells in the macaque whose firing rate depended on the location of the macaque, we note that very extensive testing with formal contrasts of different hypotheses performed along the lines described by Georges-François et al. (1999) is in general needed to show whether a cell in the primate hippocampus responds to the place where the monkey is rather than spatial view. For example, given that a region of allocentric space in a room that defines the spatial view field of a spatial view cell will not be visible from all places in a room, it is not sufficient to show that the firing rate depends on the place where the monkey is, because the spatial view does as well. Another example is shown in figure 2 of Rolls (1996b,c), of a cell (av057) that might have been interpreted as a place cell if testing with different head directions of the monkey allowing different spatial views had not been performed. It is essential to measure the firing rate of a primate hippocampal cell with different head directions so that different spatial views can be compared, as testing with just one head direction (Matsumura et al., 1999) cannot provide evidence that will distinguish a place cell from a spatial view cell. These points will need to be borne in mind in future studies of hippocampal neuronal activity in primates, and simultaneous recording of head position, head direction, and eye position, as described in this paper, will be needed. It is also necessary to test primate hippocampal cells during active locomotion, in case this is an important factor as in the rat. Having said this, we have found that spatial view cells in the primate hippocampus have similar responses during active locomotion as when the monkey is stationary but is allowed to look around and actively explore the environment with eye movements. Indeed, it is possible that this active exploration of an environment by eye movements is somewhat analogous to the active exploration which a rat does by running around. The actual recording system we use does allow the monkey very active locomotion when he is moving, in that the chair on wheels is attached only to his head, and allows head angular velocities as large as 100 degrees/s and linear motion of 0.6 m/s, so it is unlikely that this has resulted in our not finding place cells in the primate hippocampus. However, we do not have a strong position on this issue. We simply note that we have not so far observed place cells in the primate hippocampus, we note that great care would be needed to show that they are place cells if found, and we draw attention to a remarkable new type of cell, spatial view cells, which in primates respond to place "out there."

It is also useful to emphasize that spatial view cells are very different from head direction cells, which are found in the primate presubiculum and parahippocampal gyrus (Robertson et al., 1999). For example, for a given head direction, if the monkey is moved to different places in the environment where the spatial view is different, spatial view cells give different responses. In

contrast, the response of head direction cells remains constant for a given head direction, even when the spatial view is very different (Robertson et al., 1999). To provide a simple concept to emphasize the difference, one can think of head direction cells as responding like a compass attached to the top of the head, which will signal head direction even when the compass is in different locations, including in a totally different, and even novel, spatial environment.

Before discussing the possible functions of primate spatial view cells, and their relation to rat place cells, it is useful to summarize the properties of other cells in the primate hippocampus that are relevant to understanding the representation of space by the primate hippocampus.

Responses of Neurons in the Primate Hippocampus to Whole Body Motion

Another type of cell found in the primate hippocampus responds to whole body motion (O'Mara et al., 1994), an idiothetic cue. For example, such cells respond when the monkey is rotated about the vertical axis, with a much larger response for clockwise than for anti-clockwise rotation. By occluding the visual field, it was possible to show that in some cases the response of these cells required visual input. For other cells, visual input was not required, and it is likely that such cells responded on the basis of vestibular inputs. Some cells were found that responded to a combination of body motion and view or place. In some cases, these neurons respond to linear motion, in others to axial rotation ($n = 43$). In some cases, these neurons require visual input for their responses; in other cases, the neurons appear to be driven by vestibular inputs. Some cells responded to a combination of movement together with either a particular local view seen by the monkey ($n = 2$) or a particular place towards which the monkey is moving ($n = 1$). These (idiothetic) whole-body motion cells may be useful in a memory system for remembering trajectories through environments, of use for example in short range spatial navigation and path integration (O'Mara et al., 1994).

Neurons Related to Learning Associations Between Visual Stimuli and Spatial Responses

In another type of task for which the primate hippocampus is needed, conditional spatial response learning, in which the monkeys had to learn which spatial response to make to different stimuli, that is, to acquire associations between visual stimuli and spatial responses, 14% of hippocampal neurons responded to particular combinations of visual stimuli and spatial responses (Miyashita et al., 1989). The firing of these neurons could not be accounted for by the motor requirements of the task, nor wholly by the stimulus aspects of the task, as demonstrated by testing their firing in related visual discrimination tasks. These results showed that single hippocampal neurons respond to combinations of the visual stimuli and the spatial responses with which they must become associated in conditional response tasks, and are consistent with the computational theory described above according to which part of the mechanism of this learning involves associations between visual stimuli and spatial responses learned by single hippocampal neurons.

In a following study, it was found that during such conditional spatial response learning, 22% of this type of neuron analysed in the hippocampus and parahippocampal gyrus altered their responses so that their activity, which was initially equal to the two new stimuli, became progressively differential to the two stimuli when the monkey learned to make different responses to the two stimuli (Cahusac et al., 1993). These changes occurred for different neurons just before, at, or just after the time when the monkey learned the correct response to make to the stimuli, and are consistent with the hypothesis that when new associations between objects and places (in this case for responses) are learned, some hippocampal neurons learn to respond to the new associations that are required to solve the task.

DISCUSSION

The spatial view cells we have described in this and related papers (Rolls et al., 1997a,b, 1998; Robertson et al., 1998; Georges-François et al., 1999) in the primate hippocampus are in the ways described above unlike place cells found in the rat (O'Keefe, 1979; Muller et al., 1991). 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 spatial 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 that would not depend on exactly where the monkey was, and that 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. The representation of space provided by primate hippocampal spatial view-responsive neurons may, thus, be useful in forming memories of what has been seen where, an example of an episodic memory.

The representation of space in the rat hippocampus, which is of the place where the rat is, may be related to the fact that with a much less developed visual system than the primate, the rat's representation of space may be defined more by the olfactory and tactile as well as distant visual cues present, and may thus tend to reflect the place where the rat is. An interesting hypothesis on how this difference could arise from essentially the same computational process in rats and monkeys is as follows. The starting assumption is that in both the rat and the primate, the dentate granule cells and the CA3 and CA1 pyramidal cells respond to combinations of the inputs received. In the case of the primate, a combination of visual features in the environment will over a typical viewing angle of perhaps 10–20 degrees result in the formation of a spatial view cell, the effective trigger for which will thus be a combination of visual features within a relatively small part of space. In contrast,

in the rat, given the very extensive visual field which may extend over 180–270 degrees, a combination of visual features formed over such a wide visual angle would effectively define a position in space, that is a place. The actual processes by which the hippocampal formation cells would come to respond to feature combinations could be similar in rats and monkeys, involving for example competitive learning in the dentate granule cells, autoassociation learning in CA3 pyramidal cells, and competitive learning in CA1 pyramidal cells (see Rolls, 1989a,b, 1995, 1996; Treves and Rolls, 1994; Rolls and Treves, 1998). Thus spatial view cells in primates and place cells in rats might arise by the same computational process but be different by virtue of the fact that primates are foveate and view a small part of the visual field at any one time, whereas the rat has a very wide visual field. Although the representation of space in rats thus may be in some ways analogous to the representation of space in the primate hippocampus, the difference does have implications for theories of hippocampal function. In rats, the presence of place cells has led to theories that the rat hippocampus is a spatial cognitive map, and can perform spatial computations to implement navigation through spatial environments (O'Keefe and Nadel, 1978; O'Keefe, 1991; Burgess et al., 1994). The details of such navigational theories could not apply in any direct way to what is found in the primate hippocampus. Nor could place cells help in object-place memory of the type that is prototypical of primate including human hippocampal function, for in this type of memory, the location of an object in space can be learned without ever visiting that place "out there" in space. Place cells, which respond to the place where the animal is, would simply be irrelevant and inappropriate for this type of memory task, whereas primate spatial view cells are ideal for this task.

Instead, what is applicable to both the primate and rat hippocampal recordings is that hippocampal neurons contain a representation of space (for the rat, primarily where the rat is, and for the primate primarily of positions "out there" in space), which is a suitable representation for an episodic memory system. In primates, this would enable one to remember, for example, where an object was seen. In rats, it might enable memories to be formed of where particular objects (defined, e.g., by olfactory, tactile, and taste inputs) were found. Thus, at least in primates, and possibly also in rats, the neuronal representation of space may be appropriate for forming memories of particular events (each of which usually has a spatial component, providing one type of context). Such memories would be useful for spatial navigation, for which according to the present hypothesis the hippocampus would implement the memory component but not the spatial computation component. A detailed and quantitative model of how the hippocampus could operate as a memory system, and of how information stored in the hippocampus could be recalled, has been developed elsewhere (Rolls, 1989a,b, 1995, 1996a; Treves and Rolls, 1994; Rolls and Treves, 1998; Rolls et al., 1997b; Treves, Rolls and Simmen, 1997; Schultz and Rolls, 1999).

Some of the cells with spatial responses in the primate hippocampus and presubiculum described here could be involved in functions other than purely episodic memory. For example, head direction and whole body motion neurons could be useful as part of a system for remembering the compass bearing (head direction) and distance travelled, to enable one, for example, to find one's way back to the origin, even with a number of sectors of travel, and over a number of minutes. This is referred to as path integration. Spatial memory and navigation can also benefit from visual information about places being looked at, which can be used as landmarks, and spatial view cells added to the head direction cells and whole body motion cells would provide the basis for a good memory system useful in navigation. Another possibility is that primate head direction cells are part of a system for computing during navigating which direction to head towards next. For this, not only would a memory system be needed of the type elaborated elsewhere (Rolls, 1989a,b, 1996a; Treves and Rolls, 1994; Rolls and Treves, 1998) that can store spatial information of the type found in the hippocampus, but also an ability to use this information in spatial computation of the appropriate next bearing would be needed. Such a system might be implemented using a hippocampal memory system, which associated together spatial views, whole body motion, and head direction information. The findings described here certainly implicate the hippocampus in the update of spatial view cells' firing produced in the dark by idiothetic cues including eye position and head direction signals. The system would be different from that in the rat (Burgess et al., 1994; McNaughton et al., 1996), in that spatial view is represented in the primate hippocampus.

The studies described here provide fundamental evidence about the information represented in the primate hippocampus, and are of considerable interest in relation to understanding what the primate (including human) hippocampus does, and how it works as a memory system (Rolls and Treves, 1998). Indeed, the relevance to humans of this work in primates is attested to by the fact that neuroimaging studies in humans are showing that the sight of simple spatial views can activate hippocampus-related areas (e.g., Epstein and Kanwisher, 1998). However, it is only at the neuronal level that one can address issues such as the spatial coordinate frame used (Georges-François et al., 1999), how the information is represented (which has important implications for how it is stored) (see Rolls et al., 1998), and how similar the recall state is to the stored memory state when retrieval occurs to a partial cue (Robertson et al., 1998). It would be difficult with neuroimaging studies to show, for example, that there is an allocentric representation of space "out there" that is accessed either by looking at the particular location in space, or by rotating the head and moving the eyes to another head direction/eye position (and even head position) combination that will result in looking towards that location in space when the view details are made invisible. Nor can such neuroimaging studies show that, for example, other neurons in the hippocampus respond to whole body motion, which for some neurons is based on vestibular signals, for other neurons on optical flow signals, and for other neurons on either. Analyses at the neuronal level are thus essential because they provide clear evidence about what is being represented in a brain structure, and are also especially relevant to understanding how a part of the brain operates, because they show

what information is being exchanged between the computing elements of the brain (Rolls and Treves, 1998).

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REFERENCES

Amaral DG. 1987. Memory: anatomical organization of candidate brain regions. In: Mountcastle VB, editor. Handbook of physiology. Section 1, the nervous system. Vol. V: higher functions of the brain. Part 1. Washington, DC: American Physiological Society 7:211–294.

Andersen RA. 1995. Coordinate transformations and motor planning in posterior parietal cortex. In: Gazzaniga MS, editor. The cognitive neurosciences. Cambridge, MA: MIT Press 519–532.

Burgess N, Recce M, O'Keefe J. 1989. A model of hippocampal function. Neural Networks 7:1065–1081.

Cahusac PMB, Miyashita Y, Rolls ET. 1989. Responses of hippocampal formation neurons in the monkey related to delayed spatial response and object-place memory tasks. Behav Brain Res 33:229–240.

Cahusac PMB, Rolls ET, Miyashita Y, Niki H. 1993. Modification of the responses of hippocampal neurons in the monkey during the learning of a conditional spatial response task. Hippocampus 3:29–42.

Epstein R, Kanwisher N. 1998. A cortical representation of the local visual environment. Nature 392:598–601.

Feigenbaum JD, Rolls ET. 1991. Allocentric and egocentric spatial information processing in the hippocampal formation of the behaving primate. Psychobiology 19:21–40.

Foster TC, Castro CA, McNaughton BL. 1989. Spatial selectivity of rat hippocampal neurons: dependence on preparedness for movement. Science 244:1580–1582.

Gaffan D. 1987. Amnesia, personal memory and the hippocampus: experimental neuropsychological studies in monkeys. In: Stahl SM, Iversen SD, Goodman EC, editors. Cognitive neurochemistry. Oxford: Oxford University Press, 46–56.

Gaffan D. 1994. Scene-specific memory for objects: a model of episodic memory impairment in monkeys with fornix transection. J Cogn Neurosci 6:305–320.

Gaffan D, Harrison S. 1989a. A comparison of the effects of fornix section and sulcus principalis ablation upon spatial learning by monkeys. Behav Brain Res 31:207–220.

Gaffan D, Harrison S. 1989b. Place memory and scene memory: effects of fornix transection in the monkey. Exp Brain Res 74:202–212.

Gaffan D, Saunders RC. 1985. Running recognition of configural stimuli by fornix transected monkeys. Q J Exp Psychol 37B:61–71.

Georges-François P, Rolls ET, Robertson RG. 1999. Spatial view cells in the primate hippocampus: allocentric view not head direction or eye position or place. Cereb Cortex 9:197–212.

Markus EJ, Qin YL, Leonard B, Skaggs W, McNaughton BL, Barnes CA. 1995. Interactions between location and task affect the spatial and directional firing of hippocampal neurons. J Neurosci 15:7079–7094.

Matsumura N, Nishijo H, Tamura R, Eifuku S, Ono T. 1999. Spatial- and task-dependent neuronal responses during real and virtual translation in the monkey hippocampal formation. J Neurosci 19:2381–2393.

McNaughton BL, Barnes CA, O'Keefe J. 1983. The contributions of position, direction, and velocity to single unit activity in the hippocampus of freely-moving rats. Exp Brain Res 52:41–49.

McNaughton BL, Barnes CA, Gerrard JL, Gothard K, Jung MW, Knierim JJ, Kudrimoti H, Qin Y, Skaggs WE, Suster M, Weaver KL. 1996. Deciphering the hippocampal polyglot: the hippocampus as a path integration system. J Exp Biol 199:173–185.

Miyashita Y, Rolls ET, Cahusac PMB, Niki H, Feigenbaum JD. 1989. Activity of hippocampal neurons in the monkey related to a conditional spatial response task. J Neurophysiol 61:669–678.

Muller RU, Kubie JL, Bostock EM, Taube JS, Quirk GJ. 1991. Spatial firing correlates of neurons in the hippocampal formation of freely moving rats. In: Paillard J, editor. Brain and space. Oxford: Oxford University Press, 296–333.

O'Keefe J. 1979. A review of the hippocampal place cells. Prog Neurobiol 13:419–439.

O'Keefe J. 1984. Spatial memory within and without the hippocampal system. In: Seifert W, editor. Neurobiology of the hippocampus. London: Academic Press 375–403.

O'Keefe J. 1991. The hippocampal cognitive map and navigational strategies. In: Paillard J, editor. Brain and space. Oxford: Oxford University Press 273–295.

O'Keefe J, Nadel L. 1978. The hippocampus as a cognitive map. Oxford: Clarendon Press.

O'Mara SM, Rolls ET, Berthoz A, Kesner RP. 1994. Neurons responding to whole-body motion in the primate hippocampus. J Neurosci 14:6511–6523.

Ono T, Nakamura K, Nishijo H, Eifuku S. 1993. Monkey hippocampal neurons related to spatial and nonspatial functions. J Neurophysiol 70:1516–1529.

Panzeri S, Schultz SR, Treves A, Rolls ET. 1999. Correlations and the encoding of information in the nervous system. Proc R Soc B 266:1001–1012.

Parkinson JK, Murray EA, Mishkin M. 1988. A selective mnemonic role for the hippocampus in monkeys: memory for the location of objects. J Neurosci 8:4059–4167.

Petrides M. 1985. Deficits on conditional associative-learning tasks after frontal- and temporal-lobe lesions in man. Neuropsychologia 23:601–614.

Robertson RG, Rolls ET, Georges-François P. 1998. Spatial view cells in the primate hippocampus: Effects of removal of view details. J Neurophysiol 79:1145–1156.

Robertson RG, Rolls ET, Georges-François P. 1999. Head direction cells in the primate presubiculum. Hippocampus 9:206–219.

Rolls ET. 1989a. Functions of neuronal networks in the hippocampus and neocortex in memory. In: Byrne JH, Berry WO, editors. Neural models of plasticity: experimental and theoretical approaches. San Diego: Academic Press 240–265.

Rolls ET. 1989b. The representation and storage of information in neuronal networks in the primate cerebral cortex and hippocampus. In: Durbin R, Miall C, Mitchison G, editors. The computing neuron. Wokingham, England: Addison-Wesley 125–159.

Rolls ET. 1995. A model of the operation of the hippocampus and entorhinal cortex in memory. Int J Neural Systems 6(Suppl):51–70.

Rolls ET. 1996a. A theory of hippocampal function in memory. Hippocampus 6:601–620.

Rolls ET. 1996b. The representation of space in the primate hippocampus, and episodic memory. In: Ono T, McNaughton BL, Molotchnikoff S, Rolls ET, Nishijo H, editors. Perception, memory and emotion: frontier in neuroscience. Amsterdam: Elsevier 375–400.

Rolls ET. 1996c. The representation of space in the primate hippocampus, and its relation to memory. In: Ishikawa K, McGaugh JL, Sakata H, editors. Brain processes and memory. Amsterdam: Elsevier 203–227.

Rolls ET, O'Mara S. 1993. Neurophysiological and theoretical analysis of how the hippocampus functions in memory. In: Ono T, Squire LR, Raichle ME, Perrett DI, Fukuda M, editors. Brain mechanisms of

perception and memory: from neuron to behavior. New York: Oxford University Press 276–300.
Rolls ET, O'Mara SM. 1995. View-responsive neurons in the primate hippocampal complex. Hippocampus 5:409–424.
Rolls ET, Treves A. 1998. Neural networks and brain function. Oxford: Oxford University Press.
Rolls ET, Miyashita Y, Cahusac PMB, Kesner RP, Niki H, Feigenbaum J, Bach L. 1989. Hippocampal neurons in the monkey with activity related to the place in which a stimulus is shown. J Neurosci 9:1835–1845.
Rolls ET, Robertson RG, Georges-François P. 1997a. Spatial view cells in the primate hippocampus. Eur J Neurosci 9:1789–1794.
Rolls ET, Treves A, Foster D, Perez-Vicente C. 1997b. Simulation studies of the CA3 hippocampal subfield modelled as an attractor neural network. Neural Networks 10:1559–1569.
Rolls ET, Treves A, Robertson RG, Georges-François P, Panzeri S. 1998. Information about spatial view in an ensemble of primate hippocampal cells. J Neurophysiol 79:1797–1813.
Rupniak NMJ, Gaffan D. 1987. Monkey hippocampus and learning about spatially directed movements. J Neurosci 7:2331–2337.
Schultz S, Rolls ET. 1999. Analysis of information transmission in the Schaffer collaterals. Hippocampus. In press.
Smith ML, Milner B. 1981. The role of the right hippocampus in the recall of spatial location. Neuropsychologia 19:781–793.
Suzuki W, Amaral DG. 1994. Topographic organisation of the reciprocal connections between the monkey entorhinal cortex and the perirhinal and parahippocampal cortices. J Neurosci 14:1856–1877.
Treves A, Rolls ET. 1994. A computational analysis of the role of the hippocampus in memory. Hippocampus 4:374–391.
Treves, A, Rolls ET, Simmen, M. 1997. Time for retrieval in recurrent associative memories. Physica D 107:392–400.
Van Hoesen GW. 1982. The parahippocampal gyrus. New observations regarding its cortical connections in the monkey. Trends Neurosci 5:345–350.
Watanabe T, Niki H. 1985. Hippocampal unit activity and delayed response in the monkey. Brain Res 325:241–254.