Spatial View Cells in the Primate Hippocampus: Allocentric View not Head Direction or Eye Position or Place

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Hippocampal function was analysed by making recordings from hippocampal neurons in monkeys actively walking in the laboratory. 'Spatial view' cells, which respond when the monkey looks at a part of the environment, were analysed. It is shown that these cells code for the allocentric position in space being viewed and not for eye position, head direction or the place where the monkey is located. 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.

Introduction

In rats, the spatial representation provided by hippocampal neurons that has been described relates to the place where the rat is (McNaughton *et al.*, 1983; O'Keefe and Speakman, 1987). A theory that the hippocampus is a computer for spatial navigation, computing bearings and distances to the next place has been built on the basis of the properties of rat place cells (Burgess *et al.*, 1994). Because it is not clear whether the primate hippocampus should be considered a spatial computer, with perhaps place cells like those of rats (Ono *et al.*, 1993), or is instead a structure involved in storing memories including memories with a spatial component such as where an object has been seen (e.g. Rolls, 1996; Rolls and Treves, 1998), we recorded from single hippocampal neurons while monkeys were moved to different places in a cue-controlled spatial environment. We found 'spatial view' cells which responded to the position in space which a monkey could see, rather than to the place where the monkey was (Rolls and O'Mara, 1995). However, because it is only during active locomotion that the place fields of rat hippocampal neurons become evident (Foster *et al.*, 1989), we set up a recording situation to allow active walking by the monkey in a rich spatial environment. We again found 'spatial view' cells that responded when the monkey looked at one part of the environment, but not when he looked at another (Rolls *et al.*, 1995, 1997a, 1998a; Robertson *et al.*, 1998).

The new investigation described here is designed to analyze whether these 'spatial view' cells respond on the basis of the allocentric position in space being viewed rather than of head direction, or eye position in the orbit, or the place where the monkey is located. [The eye position in the orbit refers to the horizontal and vertical angles of the eye in its orbit, which define where the eye is looking with respect to the head. The head direction is defined as the angle between the direction the head is facing and a fixed reference direction in space (which might be geographical north). Allocentric refers to coordinates relative to a system which is not the head axis, i.e. allocentric refers to world- (or room-) centered coordinates.] That is, the aim of the experiments described here is to examine the spatial coordinate system used by spatial view cells: do they respond in egocentric

coordinates (e.g. position relative to the head or body, or reflecting a combination of retinal and eye position) as has been found for previous spatial representations examined neurophysiologically in primates, or do they respond in allocentric coordinates (e.g. to a spatial location in the room)? We show here that they respond in allocentric coordinates, and are relevant to understanding how humans can remember objects seen in particular spatial locations that have been seen but never visited, by revealing the type of spatial coordinate system used by these cells in the hippocampus, a brain region implicated in this type of episodic memory in primates, including humans. The new analyses described here are on the spatial coordinates being used by these cells. A previous paper (Robertson *et al.*, 1998) addressed the issue of the effect of removal of the view details on the responses of these neurons. This series of studies is being performed in order to understand the operation of the hippocampus and connected areas in memory and spatial function in health and disease (see Scoville and Milner, 1957; Gaffan, 1994; Squire and Knowlton, 1994).

Materials and Methods

To perform the experiments we arranged for the monkey to see positions in space with different head directions, with different eye positions and when the animal was located at different positions in the laboratory. The recordings were made both during active locomotion and when the monkey was still for a few seconds visually exploring the environment by eye movements. The neuronal activity for a cell was sorted according to each hypothesis to be tested (allocentric view, place, eye position and head direction), and an ANOVA was performed to determine whether the cell had significantly different firing rates when sorted according to each of the hypotheses. In addition, the quantitative measure of the information that was available in the firing rate of the cell about the different spatial hypotheses was calculated. We were able to show, for example, that these cells convey much more information about the spatial view than about the place where the monkey is, or about eye position, or about head direction.

Recordings

Single neurons were recorded with glass-insulated tungsten microelectrodes from two male rhesus macaques (3–5 kg) with methods that have been described previously (Rolls *et al.*, 1989). [All procedures 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 monkey was free to walk on all fours with his head in a forward looking position round an open 4×4 m laboratory in a 2.7×2.7 m area in a modified chair on four wheels. A plan of the laboratory, which contained a door, racks of neurophysiological apparatus, a work bench, etc., is shown in Figure 3. The head orientation was fixed with respect to the chair, so that the head orientation and position at all times could be monitored by tracking the chair position and orientation (see below). The chair had a removable bottom, so that testing could take place both during active locomotion on all fours by the monkey, and with the monkey stationary in the environment. Three of the cups were provided

with food to encourage the monkey to learn about feeding places in the spatial environment. Small pieces of food were also sometimes scattered on the floor, to ensure that the monkey explored the environment fully. The monkeys were very mobile during the experiments, searching for, picking up and eating small pieces of food placed on given trials in only some of the fixed cups or on the floor, and also exploring fully the laboratory. Although they frequently moved in this way round the environment with linear velocities as great as 0.6 m/s, and head angular velocities as great as 100°/s (see Rolls *et al.*, 1997a, 1998a), they also spent some of each session sitting quietly on the floor, looking at different parts of the laboratory. Eye position was measured with the search coil technique, with the field coils attached to the walker to which the head was also attached. The eye movements made by the monkey were ~35° left and right, and ~35° up and down, with respect to head direction. The head direction and position in the room were measured using a video tracking device (Datawave, Tucson, AZ) with the camera in the ceiling tracking two light-emitting diodes placed in line 25 cm apart above the head on the top of the chair. A new coordinate for the position of the monkey's head in the room was provided every 17 ms. The rear light-emitting diode flashed at one-quarter of the frame rate of the tracker acquisition system, in order to enable the front of the chair to be distinguished from the rear. We wrote software to provide every 25 ms the position of the monkey's head in the room, the head direction, the eye position (i.e. the angle horizontally and vertically of the eyes with respect to the head), and from these the position on the wall of the room at which the monkey was looking. Every time that the cell fired, that time was recorded with an accuracy of 1 ms. The Datawave spike-cutting software was used offline to ensure that the spikes of well-isolated neurons were analysed. Software was written to measure the firing rate of the neuron whenever the monkey was looking at a position in space. The algorithm took a fixed length record (500 ms long for the analyses described in this paper) whenever the eyes were still (to within typically 1°) during the record, and calculated the firing rate together with where the monkey was looking during that record. The next record was taken immediately after the preceding one, if there was no eye movement. (The findings described in this paper were unaffected if alternatively a new record was taken only when a new eye movement was made.) The algorithm could lag its neuronal data collection a short latency later than the eye position data. (If the neuron started to respond 100 ms after the monkey moved his eyes to an effective location in space, this lag could be set to 100 ms. In practice, the lag was set for all neurons to a value of 50 ms.) From the records containing a firing rate and the place of the monkey, the head direction and the eye position, it was possible to plot diagrams and perform statistical and information theoretic analyses of the firing rate of the cell when different locations in the room were being viewed, and also in relation to eye position, place and head direction. For allocentric position, the records were binned typically into 64 bins horizontally (16 for each wall) and 16 vertically. For the information analysis, the data were further quantized into typically 16 bins, in order to provide the numbers of samples needed for the information analyses. With an average recording time for any given statistical analysis of 2.76 min, the average total number of spikes recorded from a spatial view cell was 465 spikes, leading to the average rate of a spatial view cell during these experiments of 2.8 spikes/s. (For comparison, it is of interest to note that the average firing rate of the spatial view cells described here during locomotion when the monkey is visually exploring all parts of the environment is ~1.8 spikes/s, compared to the spontaneous rate of 0.6 spikes/s.) The sampling of the different parts of the walls and of positions in the room was rather full, as shown for example in Figure 1. The accuracy of the eye position data was ±3° (measured in a visual fixation task or using tracking of stimuli over a known visual angle), of the measurement of the chair orientation 5°, and of the chair position 5 cm for 90% of the active locomotion area.

Procedure

Cells were searched for while the monkey was actively locomoting. Cells which appeared to respond to spatial view were selected for the experiments described in this paper. Once found, sufficient experiments on a cell were performed to test as many of the hypotheses as possible for that cell.

With this overall protocol, two types of experiment were performed. In the first type of experiment, the firing rate of hippocampal cells was measured when the monkey was walking round (or was moved to different places in) the environment. The firing rate was typically measured throughout a 5–10 min period for each condition during which the monkey walked round the environment, often picking up small pieces of food scattered on the floor to encourage exploration of all parts of the environment, or visiting four small cups on the floor to which small portions of food were placed every few minutes. An advantage of this type of experiment is that the spatial view fields were being studied during active locomotion by the monkey.

In the second type of experiment the firing rate of the neuron was measured when the monkey's chair was stationary in a particular position in the environment, facing in a particular direction (with the monkey's feet touching a floor of his walker, not the lab floor, so that the monkey did not locomote). The eye position as well as the firing rate and the head direction and place were recorded for several minutes. Then the procedure was repeated for a number of different head positions and directions. The advantage of this type of experiment was that the experimenter could define by selecting the head position and direction the spatial view that was seen by the monkey, and could concentrate the data collection on a number of different head position and head direction combinations, to test hypotheses such as that the firing of the neuron depended on the spatial view being seen by the monkey, rather than the place where the monkey was located. Examples of data collection with this type of experiment are included in Figures 2 and 3. It is important to appreciate that not all spatial views can be seen from all places in an environment. For example, if the monkey was at the door shown in Figure 3, it could not see the spatial view which included cup 3 (c3), because of the apparatus shown. For this reason, the experiments were typically designed to include at least two spatial views, at least two different head directions and at least two well-separated places where the monkey was located (as illustrated in Figs 2 and 3), so that the parameter (spatial view versus head direction versus eye position versus place) which produced the most statistically significant difference in the neuronal response, and about which the cell provided the most information, could be quantified. We included in the different testing conditions at least two places from which at least two spatial views could be seen. For a spatial view cell, if data were obtained from two places, from only one of which the spatial view was visible, then this would not be a test of the coordinate frame being used by the cell.

For statistical analysis of the responses of the neurons, 4–50 values of the firing rate for each condition (e.g. direction in which the head was facing, eye position, place and spatial position at which the eyes were looking) were obtained. A one-way analysis of variance was then performed, to determine whether there were significant differences between the conditions. In some cases, as shown in Figures 2 and 3, tests of a hypothesis required comparison of certain conditions. For example, to test whether a cell responded differently to different head directions, a good comparison was to compare the rates statistically for at least two different head directions for each of which (because of different eye positions or places of the monkey) the monkey could see the location in the environment that made the cell respond. The use of these different comparisons is made clear in the Results section when actual data are described. The advantage of the one-way ANOVAs was that all available data could be included in a test of a hypothesis, which could not necessarily be included in a two-way ANOVA, where one factor might be spatial view, and another place. For example, data from a particular place from which a particular spatial view could not be seen or was not looked at was relevant to testing whether a cell fired differently at different places, but was not relevant to testing whether a cell fired differently when the monkey looked at different spatial views. However, in some cases it was possible to perform two-way ANOVAs on a subset of the data in which one factor was spatial view and another place, and all such two-way ANOVAs had significant ($P < 0.05$) effects of spatial view even on the data subset, so that the effects examined in the one-way ANOVAs were not due to statistical fluctuation. In addition to performing one-way ANOVAs to test for significant differences in neuronal firing rate for the different conditions, the information the neuron conveyed about each parameter (head direction, eye position, etc.) was also calculated as follows.

Information Available in the Responses of Single Neurons

The principles of the information theoretic analysis for single neurons were similar to those developed by Richmond and Optican (1987) and Optican and Richmond (1987), except that we applied a novel correction procedure for the limited number of trials. The analytical correction procedure we use was developed by Treves and Panzeri (1995) and Panzeri and Treves (1996), to which we refer for a detailed discussion, and its efficacy in eliminating the limited sampling bias was recently compared with that of an alternative empirical procedure by Golomb *et al.* (1997). As in Rolls *et al.* (1997b), a novel aspect of the data analysis described here is that we investigated how much information was available about each stimulus in the set. The information theoretic analyses described and used here were based on the information available from the firing rate measured in 500, 100 and 25 ms periods when the eyes were steadily fixating a position in the room.

If each stimulus, *s*, were to evoke its own response, *r* (or its own set of unique responses), then upon measuring *r* one would ascertain *s*, and thus gain $I(s) = -\log_2 P(s)$ bits of information, where $P(s)$ is the probability of occurrence of a particular stimulus (in this case, a location in space) *s*. If instead, as happens in general, the same response can sometimes be shared, with different probabilities, by several stimuli, the probabilistic stimulus–response relation will be expressed by a table of probabilities $P(s,r)$, or, equivalently, of conditional probabilities $P(r|s) = P(s,r)/P(s)$. The information about *s* gained by knowing *r* can be evaluated from the formula

$$I(s, R) = \sum_r P(r|s) \log_2 \frac{P(r|s)}{P(r)} \qquad (1)$$

[This can be regarded as the difference between the original uncertainty about *s* (or *a priori* entropy) and the residual uncertainty after *r* is known, and attains its maximum value $I(s) = -\log_2 P(s)$ only if the probabilistic relation reduces to the deterministic one $P(s|r) = 1$ for $s = s(r)$, and $P(s|r) = 0$ otherwise.]

Averaging over different stimuli *s* in the set of stimuli *S* one obtains the average information gain about the set of stimuli *S* present in the neuronal spike data *R* (where *R* denotes the set of responses *r*) as:

$$I(S, R) = \sum_s P(s) I(s, R) = \sum_{s,r} P(s,r) \log_2 \frac{P(s,r)}{P(s)P(r)} \qquad (2)$$

In the Results we show $I(S,R)$, the average information across all conditions or stimuli (e.g. different spatial views) that is provided about which of the set of stimuli was presented; and the maximum value I_{max} of $I(s_i, R)$, the information available in the responses of the cell about each individual condition or stimulus s_i.

In evaluating the information content from the data recorded, the neuronal responses were simply quantified by the number of spikes within any 500 ms time period, as stated above, i.e. we used a uni-dimensional measure based on a firing rate measurement. While both the set of stimuli *S* and the set of responses *R* could in general be continua (and the information *I* in the relation between the two would still be well defined because of the finite resolution with which responses can help discriminate among stimuli), in practice to evaluate *I* it is convenient to discretize both stimuli and responses, and the number of discrete bins in each space must not be too high for limited sampling effects not to bias, even after the correction procedure we apply, information estimates based on limited data (Treves and Panzeri, 1995). In our analysis *S* is discretized into 16 spatial bins as explained above, and there is no need to discretize *R* because *R* is effectively already discretized into a suitably low number of bins. (This is because by measuring responses as the number of spikes in 500 ms or less, these spike counts never exceeded 15–20 for hippocampal cells with their low rates.)

The procedure introduced so far for estimating information values [from the probability table $P(s,r)$] must be supplemented by a procedure that corrects the raw estimates for their limited sampling biases. Because of the limited number of trials that can be collected, the various probability tables are not available, and one can at best approximate them

with frequency tables, e.g. $P_N(s,r)$, computed on the basis of a (limited) number of trials *N*. If *N* is very large, the frequencies should get close to the underlying probabilities, but for any finite *N* there will be a discrepancy that will result in an error in the estimated information gain. Because information quantities depend on probabilities not in a linear but in a greater than linear manner, the error deriving from this *limited sampling* does not cancel out on averaging many measurements; it is, instead, usually biased upward, resulting in an (average) overestimate of the information gain, as described by Tovee *et al.* (1993) and Treves and Panzeri (1995). The correction procedure applied is described by Treves and Panzeri (1995), Panzeri and Treves (1996), Rolls *et al.* (1998) and Rolls and Treves (1998), and validated by Golomb *et al.* (1997).

Recording Sites

X-radiography was used to determine the position of the microelectrode after each recording track relative to permanent reference electrodes and to the anterior sphenoidal process, a bony landmark whose position is relatively invariant with respect to deep brain structures. Microlesions (60–100 μA, 100 s) made through the tip of the recording electrode during the final tracks were used to mark the location of typical neurons. These microlesions, together with the associated X-radiographs, allowed the position of all cells to be reconstructed in the 50 μm brain sections with the methods described in Feigenbaum and Rolls (1991). As described previously the spatial view cells had very low spontaneous firing rates (typically in the range 0–2 spikes/s in the locomoting monkey, see Table 2), low peak firing rates (typically in the range 10–20 spikes/s, see Table 2) and large-amplitude broad spikes (Rolls *et al.*, 1997a, 1998a). Other cells had faster spontaneous and peak firing rates (often in the range 20–60 spikes/s), and small-amplitude short spikes. Taking into account findings in the rat (e.g. Fox and Ranck, 1981), it is likely that the large, slow-spiking cells are pyramidal cells, and the fast-firing, small-amplitude cells are interneurons. All the spatial view cells described here also had the large-amplitude, low-firing rate type of activity, and were recorded in regions in which there are pyramidal cells. They are sometimes referred to for brevity as pyramidal cells in this paper, but the criteria for inclusion in this category are those just given.

Results

It was possible to complete the types of detailed analysis of the spatial coordinate system being used by spatial view cells for 11 cells in two macaques. [The total number of cells recorded in these experiments was 354, with 125 in monkey av and 229 in az. Of these 354 cells, it was possible to analyse the activity of 40 for sufficiently long to show that they were spatial view cells (Rolls *et al.*, 1987a).] The brain regions from which these cells were sampled are shown in Figure 8, and Figure 7 shows the recording sites.

The results of experiments on one of the cells are shown in Figures 1–3, for cell az033. Figure 1*a* 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 1*b,c* in which a spot is placed on the walls where the monkey was looking only when the firing rate was >12 spikes/s, the half-maximal firing rate. The fact that the cells responded when the monkey was looking at the spatial view field in wall 3 from a large number of different places in the room is brought out in Figure 1*b*, in which every 10th cart position and horizontal gaze direction when the cell fired at >12 spikes/s are 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 >12 spikes/s is brought out in Figure 1*c*, in which every cart position and head direction for this response rate are shown.
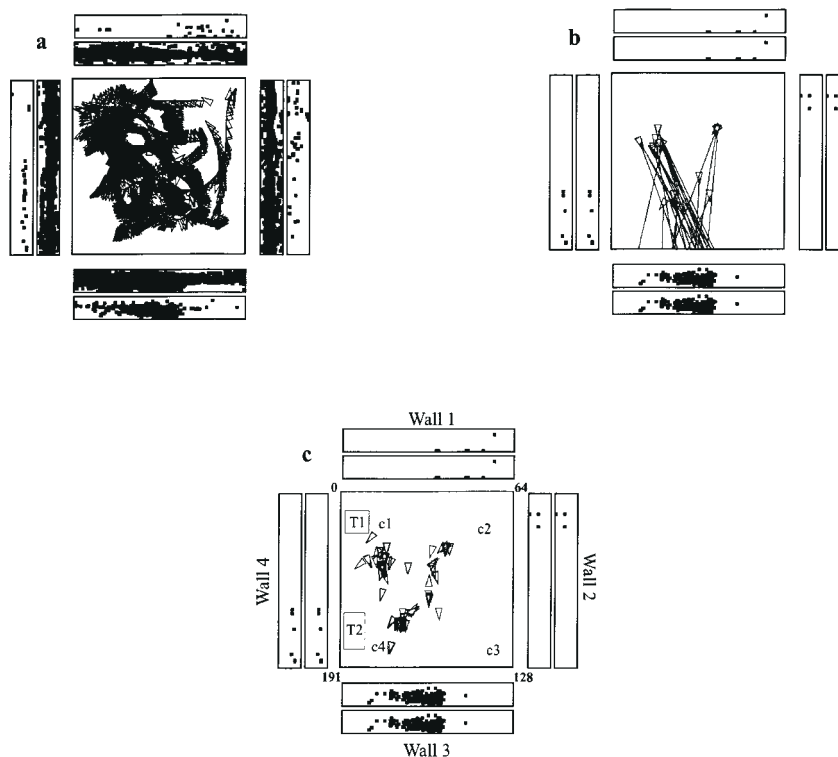
The spatial view field was also analysed with the monkey

Figure 1. 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 four rectangles, each of which represents one of the walls of the room. 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 four 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 three 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 >12 spikes/sec. A spot was placed in the rectangles whenever the cell fired at >12 spikes/s. (*c*) A similar representation of the same three 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 >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 scale printed beside the walls shows the wall horizontal coordinate system used, which is helpful in connection with Figure 4.

stationary at different places and with different head directions, as shown in Figure 2*a–d*. The range of horizontal eye positions that the monkey produced is indicated by the eye position lines and corresponding dots on the inner set of four rectangles which represent each wall, and those for which the cell fired a spike are shown in the outer set of four rectangles. It can be seen that the firing is not due to a particular eye position, or head direction or place, but instead to where the monkey looked on the wall, termed the spatial view field. Indeed, in the different testing conditions shown in Figure 2*a–d*, the spatial view field of the neuron varies little despite the large changes in eye position and place of the monkey required to view the spatial view field on the wall.

Similar points, but now showing the horizontal and vertical magnitude and shape of the spatial view field for the same neuron, are made in Figure 3*a–d* in which the darkness of the eye position plot on the left of each part of the diagram indicates the firing rate of the cell. These experiments show that the field was constant with respect to where the monkey was looking in the room, and were not just functions of head direction or eye position alone. (The point here is that the spatial view field moves in a systematic way when the place or head direction of the monkey is changed, and that the way in which it moves can be accounted for only by the allocentric spatial view hypothesis. However, to illustrate the fact that these spatial view cells are almost inactive when their effective spatial view cannot be seen at all, we show in Figure 3*e* the lack of firing when the monkey was facing away altogether from the spatial view field of the neuron.) These observations were confirmed in one-way ANOVAs, in which the several hundred firing rate and eye position data pairs used to construct Figure 3*a–d* were sorted according to different hypotheses. When the data were sorted according to where the monkey was looking on the wall (binned into eight wall positions), the one-way ANOVA was significant at $P < 0.0001$ [$F(1,7) = 12.6$], and the cell provided an average information (about spatial view) of 0.09 bits in a 500 ms epoch. When the same data were sorted according to eye position (binned into 12 bins), the one-way ANOVA was not significant [$P \approx 0.09$, $F(1,11) = 1.6$], and the cell provided an average information (about eye position) of 0.005 bits in a 500 ms epoch. When the same data were sorted according to head direction (binned into three bins), the one-way ANOVA was not significant [$P \approx 0.15$, $F(1,2) = 1.9$], and the cell provided an average information (about head direction) of 0.01 bits in a 500 ms epoch. When the same data were sorted according to the place where the monkey was located (binned into three bins), the one-way ANOVA was not significant [$P \approx 0.5$, $F(1,2) = 0.5$], and the cell provided an average information (about place) of 0.0 bits in a 500 ms epoch. These values are shown in Table 1, and the analysis leads to the conclusion that the cell responded
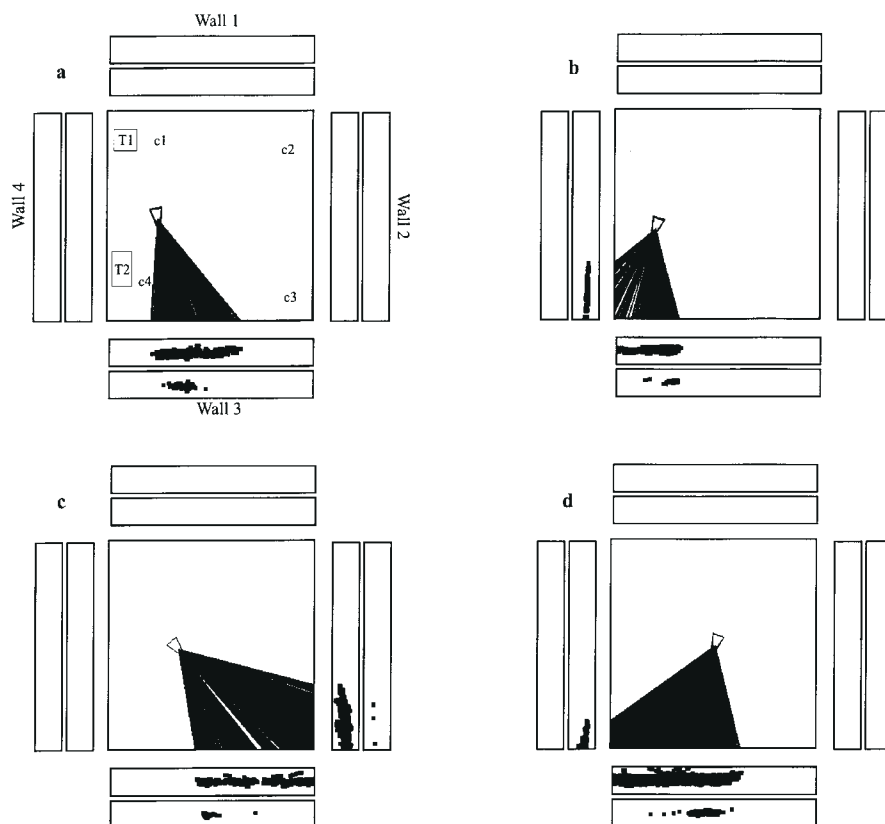
Figure 2. Examples of the firing of the same hippocampal cell (az033) as in Figure 1 when the monkey was stationary at different positions in the room, with different head directions, looking mainly at wall 3 of the room. In the four cases (a)–(d), the accumulation of the lines of sight which forms the black pattern indicates that the monkey sampled visually the whole space within its field of view. The black dots in the inner rectangle indicate the positions fixated on the walls. The dots in the outer rectangle indicate the positions on the walls being fixated whenever the cell fired a spike. These diagrams show that over a range of different positions in the room, and different eye positions, the cell fires when the monkey looks at a part of wall 3, the spatial view field. Note that in (b) the cell fires only with extreme left eye positions; and in (c) with extreme right eye positions; and that in both (b) and (c) the full extent of the spatial view field is not revealed because of the limit caused by the range of possible eye positions.

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. In an additional analysis, the firing rate was measured in the same place as in Figure 3c, but facing N (0°) or facing S (180°). The firing rate was significantly different [$P < 0.0001$, $F(1,1) = 35.1$].

Further evidence on the nature of the neuronal responses, and on how the data shown in Figures 1–3, 5 and 6 were obtained, is provided in Figure 4a, which shows the time course of the neuronal responses in relation to all the spatial parameters being measured, during a period of active locomotion. In the record showing the horizontal position at which the monkey was looking on the wall the dashed lines show the approximate extent of the spatial view field for cell az033, determined in the experiments shown in Figures 1–3. Figure 4a shows the type of data which over extended recording periods of many minutes allowed the conclusion to be reached that the cell starts firing when both the horizontal and vertical position on the wall being fixated are within certain limits (the horizontal wall position scale is greatly expanded, showing only one wall of the room, from 128–191); that the cart X and Y position in the room, and the head direction, do not account for the firing observed in the cell; and that the cell does not fire simply in relation to saccades *per suis*. Although the fact that there is a poor relation to saccades can be estimated to be the case from Figure 4a, we

performed a quantitative analysis of whether the firing rate altered in relation to saccades. We show in Figure 4b the firing rate measured in the period 200 ms before a saccade to 800 ms after it for eight directions of saccade. The data were obtained when the monkey was not looking towards the spatial view field of the neuron. It can be seen that the average firing rate in any direction of saccade was low, with the mean rate across all saccades being 0.4 spikes/s. There was no significant difference between the firing when the monkey made saccades in the different directions [$F(7,120) = 0.4$, not significant]. The polar plot in Figure 4b is scaled relative to the firing rate the neuron had when the monkey was looking towards the spatial view field (which was 21 spikes/s), to show how low the saccade-related firing was relative to the firing of the cell that was related to looking at the spatial view field.

Another example of the experiments to investigate the coordinates to which the firing of spatial view cells is related is shown in Figure 5 (cell av216). The firing of the cell as a function of horizontal and vertical eye position is shown in Figure 5a (left) with the monkey stationary at the place and with the head direction shown in Figure 5a (right). (The firing rate of the neuron was measured whenever the eyes were stationary to within 1° for >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 ~10° left and level in the vertical plane. The response field of the cell is plotted against wall 1 in Figure

Figure 3*a*
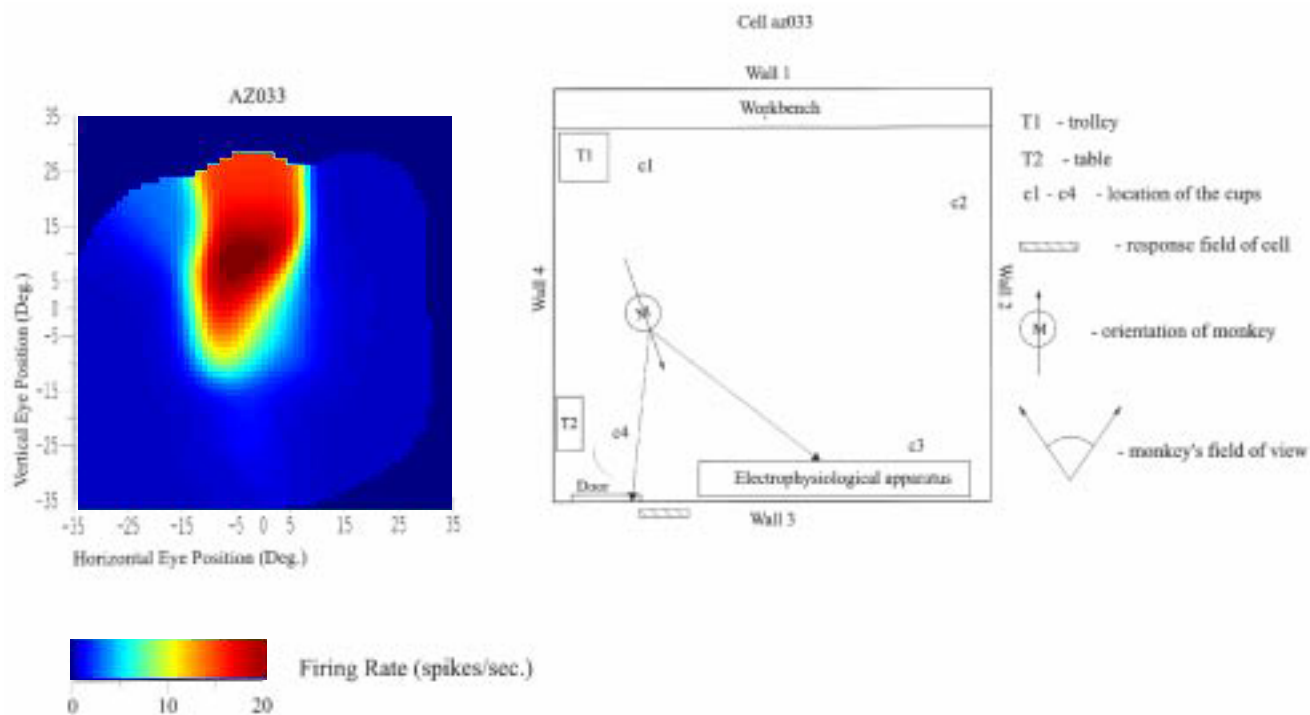

Figure 3*b*
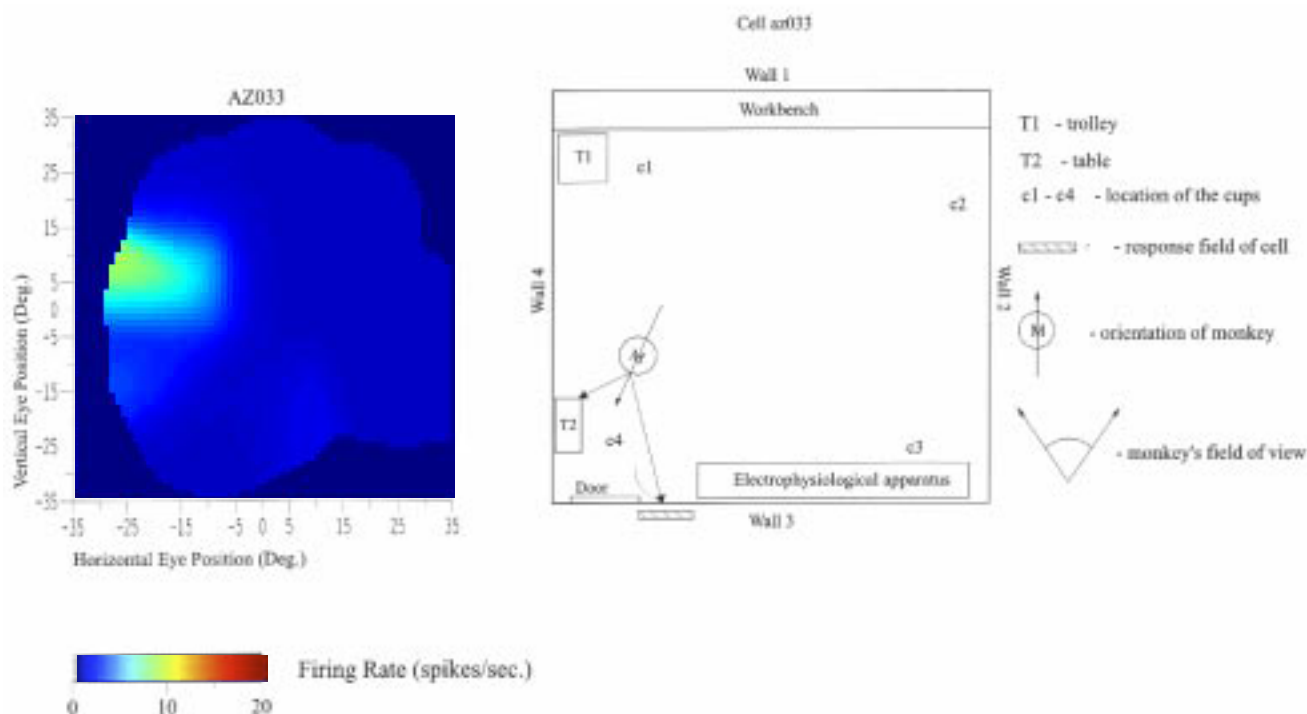
5*a* (right). The recording time for the data shown in Figure 5*a* was ~4 min. The monkey was then moved to the different place with a different head direction shown in Figure 5*b*. The highest firing rate was now when the monkey was looking ~30° right. The response field of the cell is again plotted against wall 1 in Figure 5*b* (right). (The possibility that this spatial view cell had two slightly different but close spatial view fields is a topic left for future research.) Data with the monkey at a different place (but the same head direction as in Fig. 5*b*) are shown in Figure 5*c*. The cell now fired most when the monkey looked ~30° left. The response field was, however, at the same place on wall 1 as in Figure 5*a,b*. It is clear from this type of experiment that it was
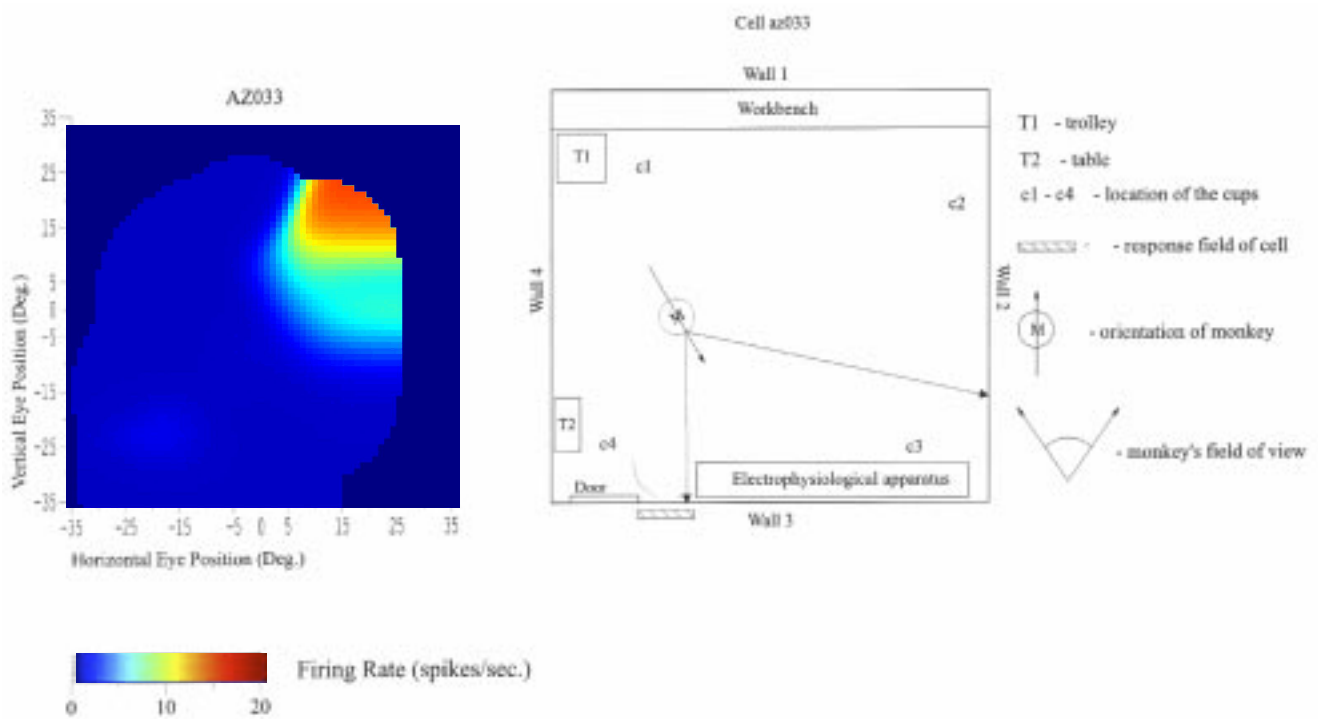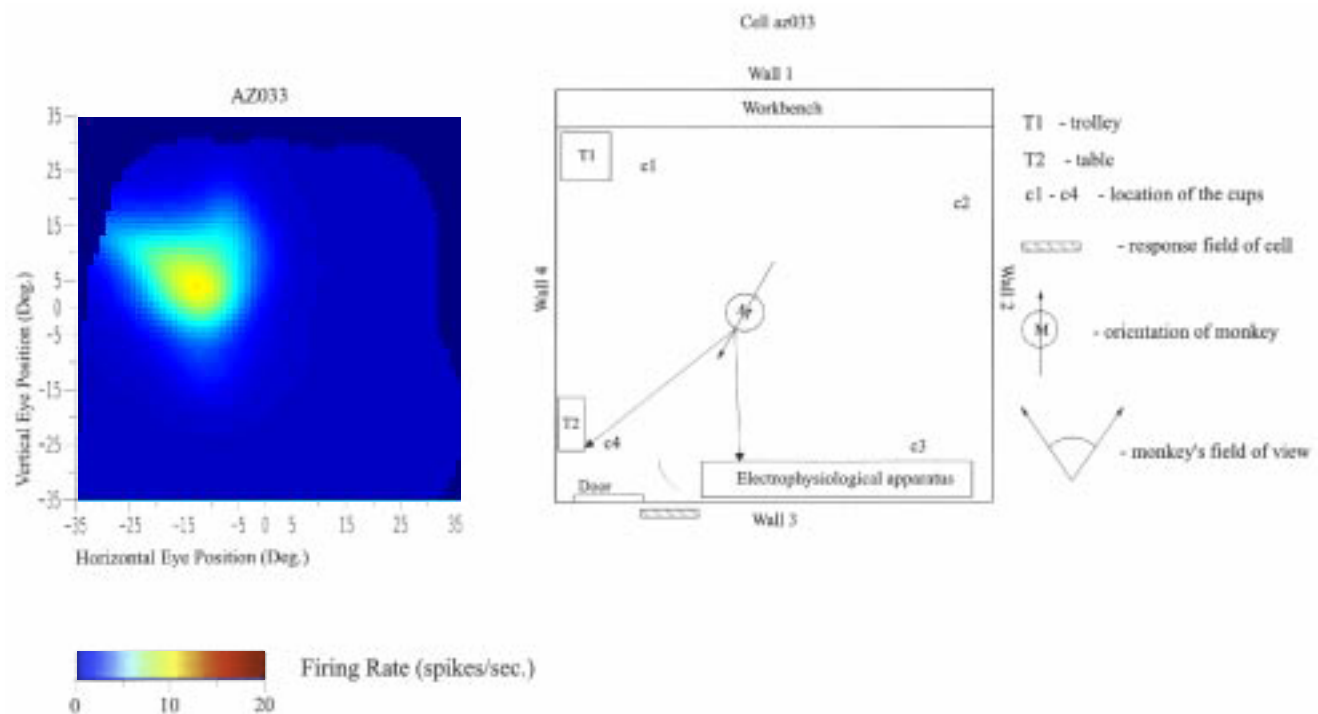
Figure 3c

Figure 3d

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 ANOVAs, in which the several hundred firing rate and eye position data pairs used to construct Figure 5a–c were sorted according to different hypotheses. When the

data for level eye position ±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 six wall positions visible in Fig. 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
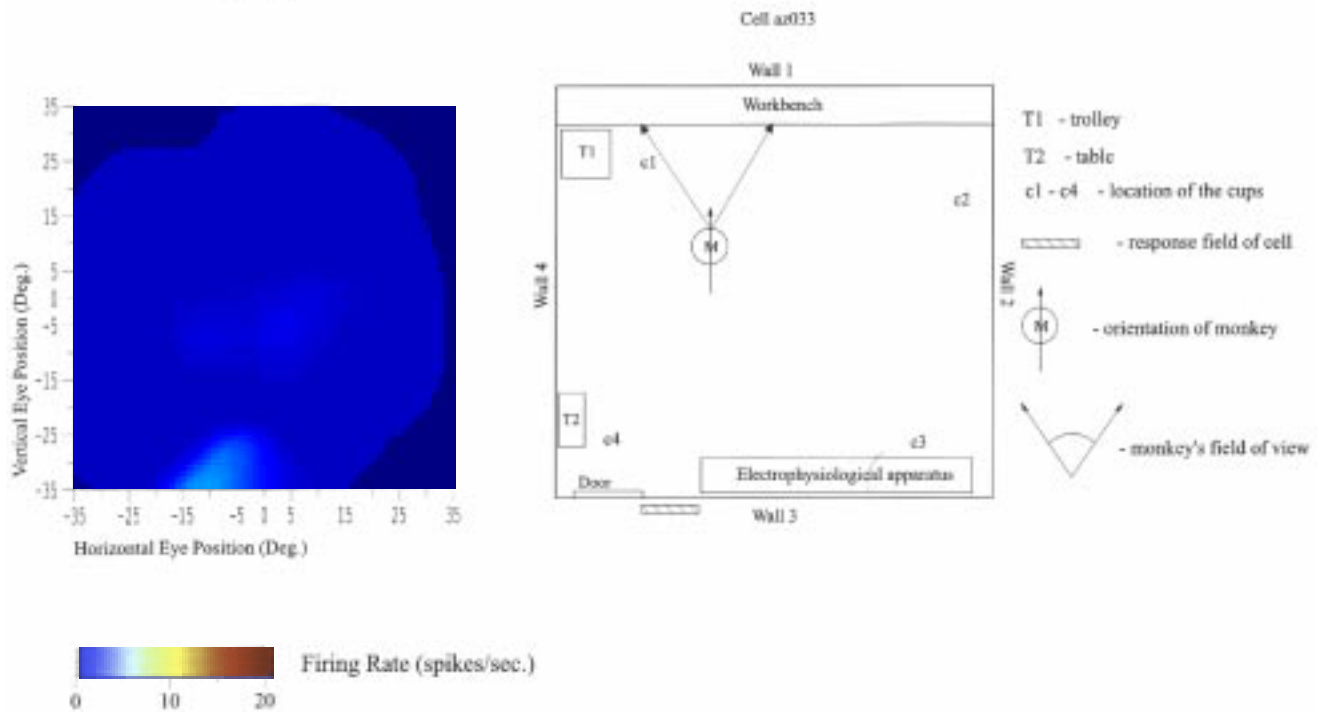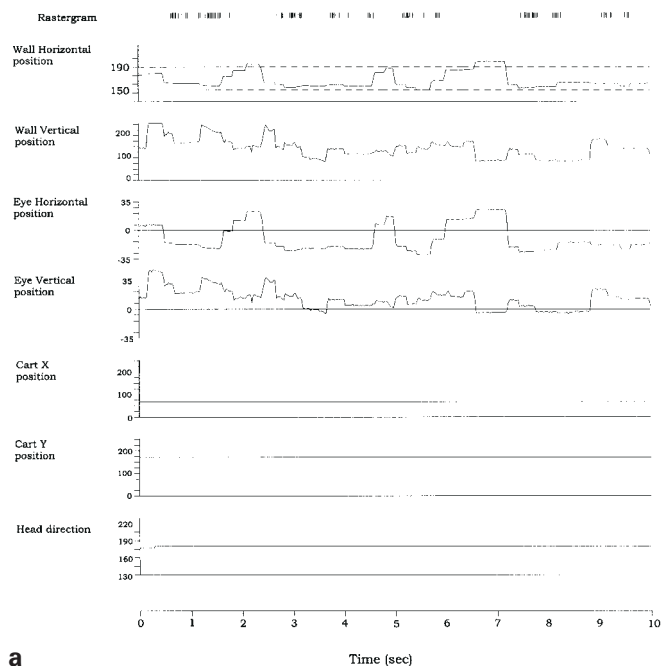
Figure 3e

Figure 3. Data obtained in the same experiments as shown in Figure 2(a)–(d), but now shown to reveal the details of the spatial view field by indicating the different firing rates as greyscale 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)–(d) Experiments with the monkey in different places, and with different head directions. (e) This shows that there was little firing of the same spatial view cell when the monkey was facing completely away from the spatial view field of the neuron.

the same data were sorted according to eye position (binned into six 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 two 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 two 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. These values are shown in Table 1, and the analysis leads to the conclusion that the cell responds significantly differently for different allocentric spatial views and has information about spatial view in its firing rate, but does not respond differently just on the basis of eye position, head direction or place.

Another example of the type of experiment shown in Figure 1–5 is shown in Figure 6, for cell av083. In this case different *vertical* angles were investigated. In Figure 6a it is shown that with the head horizontal the neuron responded when the eyes were elevated 15–30°. When the horizontal plane of the monkey's head was tilted up, the neuron responded when the eyes were less elevated, corresponding to the same position on the wall (Fig. 6b). In Figure 6c, the monkey's head was tilted down, but was so far tilted that the monkey could not see the top of the wall, and the neuron did not respond. The absence of any response in this case shows that eye position was not what

accounted for the cell's firing; it was where the animal could see in space that was important. This was confirmed in one-way ANOVAs, in which the several hundred firing rate and eye position data pairs used to construct Figure 6a,b (but in the horizontal range containing the firing) were sorted according to different hypotheses. When the data were sorted according to where the monkey was looking on the wall (binned into 11 wall positions), the one-way ANOVA was significant at $P < 0.0001$ [$F(1,10) = 8.9$], and the cell provided an average information (about spatial view) of 0.30 bits in a 500 ms epoch. When the same data were sorted according to eye position (binned into nine bins), the one-way ANOVA was not significant [$P \approx 0.09$, $F(1,8) = 1.9$], and the cell provided an average information (about eye position) of 0.03 bits in a 500 ms epoch. These values are shown in Table 1, and the analysis leads to the conclusion that the cell responds significantly differently for different allocentric spatial views and has information about spatial view in its firing rate, but does not respond differently just on the basis of eye position. The fact that the cell had different firings in Figure 6a–c even though the monkey was in the same place indicates that the cell was not responding just on the basis of place. To show that the horizontal as well as the vertical extent of the field is limited, and to show that the experiment to define the spatial coordinate system can be repeated for the horizontal plane too, we performed the experiment shown in Figure 6d. In this experiment, it is shown that when the monkey was rotated clockwise with respect to the direction in which he was facing for Figure 6a–c, the cell responded only when the monkey
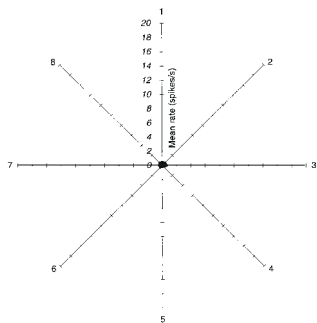
Figure 4. (*a*) A spike train recorded from the same cell as in Figures 1-3 is plotted as a function of time together with the spatial parameters measured every 25 ms during the experiment, as the monkey was looking towards the view field of the cell. The spike train is shown as a rastergram (in which each spike is represented by a vertical line) on the top line; the horizontal position of the gaze on the four walls of the room is plotted on the next line (where 0 is the lower left corner of the plans in Figs 1-3, and 63 is the upper left corner of the plans, as indicated in Fig. 1c: note that the scale has been expanded so that only a part of one of the walls is being plotted, and that the approximate horizontal extent of the spatial view field as shown in Figs 1-3 is contained within the dashed graticule lines); and the vertical position of the gaze on the next line (with 0 the bottom and 255 the top of the wall). The following lines show the horizontal and vertical eye positions (in degrees); the cart *X* and *Y* positions (where $X = Y = 0$ in the lower left of the plans, the *Y* direction is towards wall 1, and the values are in the range 0-255); and the head direction (where 0 is in the direction of the *Y* axis, the angle is measured clockwise in degrees, and the *Y* axis has been expanded to cover only a small part of the full range). (*b*) The firing rate of the same neuron measured in the period 200 ms before a saccade to 800 ms after it for eight directions of saccade. The data were obtained when the monkey was not looking towards the spatial view field of the neuron. It can be seen that the average firing rate in any direction of saccade was low, with the mean rate across all saccades being 0.4 spikes/s. (The actual values of firing rate all occur as points close to the origin of this diagram at 0 spikes/s.) The polar plot is scaled relative to the firing rate the neuron had when the monkey was looking towards the spatial view field.

looked left to where the spatial field of the neuron was located in allocentric space.

The statistical analyses that were performed on all cells are shown in Table 1. It was possible to complete the types of

detailed analysis described here for 11 cells. (The total number of cells recorded in these experiments was 354, with 125 in monkey av and 229 in az.) For all cells analysed, the cell was recorded both during active locomotion and with the monkey stationary, and the spatial view fields were similar in both conditions, as illustrated in Figures 1 and 2. For cells av232, az033, az034 and az110 the main statistical and information analyses were performed during active locomotion, and for the other cells in Table 1, they were performed with the monkey stationary, to facilitate the collection of the data required to test the different hypotheses within a circumscribed time period. (For cells av057–av216 shown at the bottom of Table 1 the analysis could be performed only within the horizontal window where the cell fired, resulting in higher information values and generally more significant ANOVAs. Another factor that resulted in higher information values for the same set of cells was that the data were collected for only a selected subset of the 16 wall positions otherwise used, and this subset spanned a few views where the cell fired strongly, and a few where it did not. The same procedure was used for the tests of all hypotheses shown in Table 1.) In all 11 cases, there were significant firing rate differences related to allocentric spatial view. In four out of four cases in which a full statistical comparison could be performed – by arranging, for example, for rate measurements to be taken when a spatial view field was on the left and then on the right of the monkey – there was no significant effect of eye position. In eight out of eight cases in which a full statistical comparison could be performed, there was no significant effect of head direction. In ten out of ten cases in which a full statistical comparison could be performed, there was no significant effect of the place where the monkey was located.

The information values that each cell provided about each parameter (spatial view, eye position, etc.) are also shown in Table 1. For each cell and for each hypothesis, the average information across conditions (e.g. the different spatial views) and the maximum information I_{max} about any one condition (e.g. about any one spatial view) are shown (see Rolls *et al.*, 1997b). For the six cells in the range av057–av216 in which the analysis could be performed in a horizontal window where the cell fired, the average information about spatial view was 0.47 bits; about eye position was 0.02 bits; about head direction was 0.05 bits; and about place was 0.03 bits. For the five cells in the range av232–az110 in which the analysis included data for all vertical positions, the average information about spatial view was 0.07 bits; about eye position was 0.004 bits; about head direction was 0.005 bits; and about place was 0.02 bits. The same pattern of results was found if the average across cells of the maximum information about any one spatial view, eye position, etc., is considered, as shown in Table 1.

The sites at which these spatial view cells were recorded are shown in Figure 7, while the extensive regions in which recordings were made and cells were sampled are shown in Figure 8. Nine of the spatial view cells analysed here were in the hippocampal pyramidal cell fields CA3 or CA1. All the cells shown in Figure 7 had allocentric encoding of spatial view, indicating that spatial view is represented in all the cell fields studied (CA3, CA1, parahippocampal gyrus and presubiculum). All the cells had low spontaneous firing rates (mean = 0.6 spikes/s, interquartile range 0.1–0.8). The peak firing rates were also relatively low (mean = 18.1 spikes/s, interquartile range 13.7–20). These characteristics, together with the large amplitude and broad action potentials, indicate that these neurons are likely to be pyramidal cells. Five cells were in the hippocampal
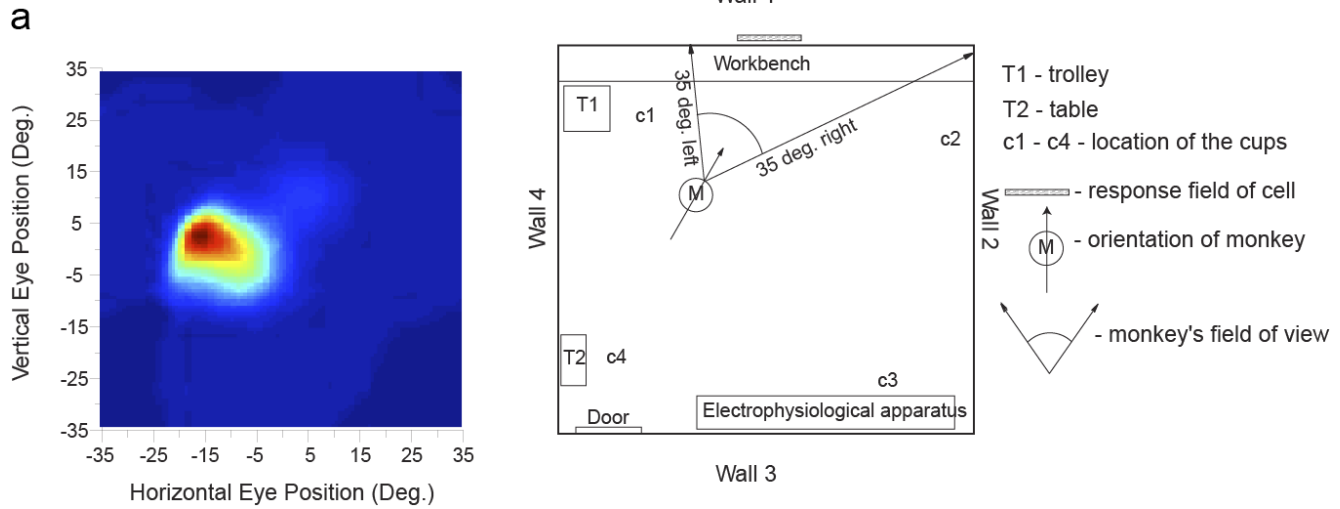
Cell av216

a

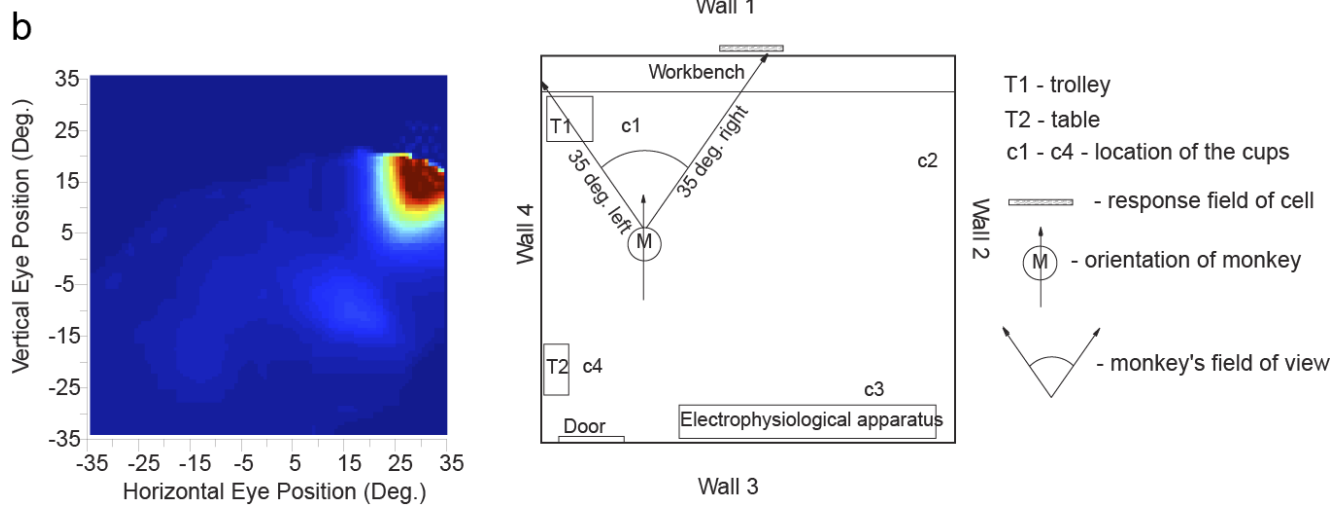
Figure 5a

b

Figure 5b

pyramidal cell field CA1, four in field CA3, one in the presubiculum and one in the parahippocampal gyrus.

Discussion

The experimental findings and quantitative analyses described here provide new evidence that the spatial coordinate system used by primate hippocampal formation spatial view cells is allocentric. The results show that these cells respond differently to different allocentrically defined parts of space at which the monkey is looking, and that these cells do not respond differently just in relation to eye position, head direction or the place where the monkey is. Correspondingly, the responses of these cells provide information about allocentric spatial view, but not about eye position, head direction or place.
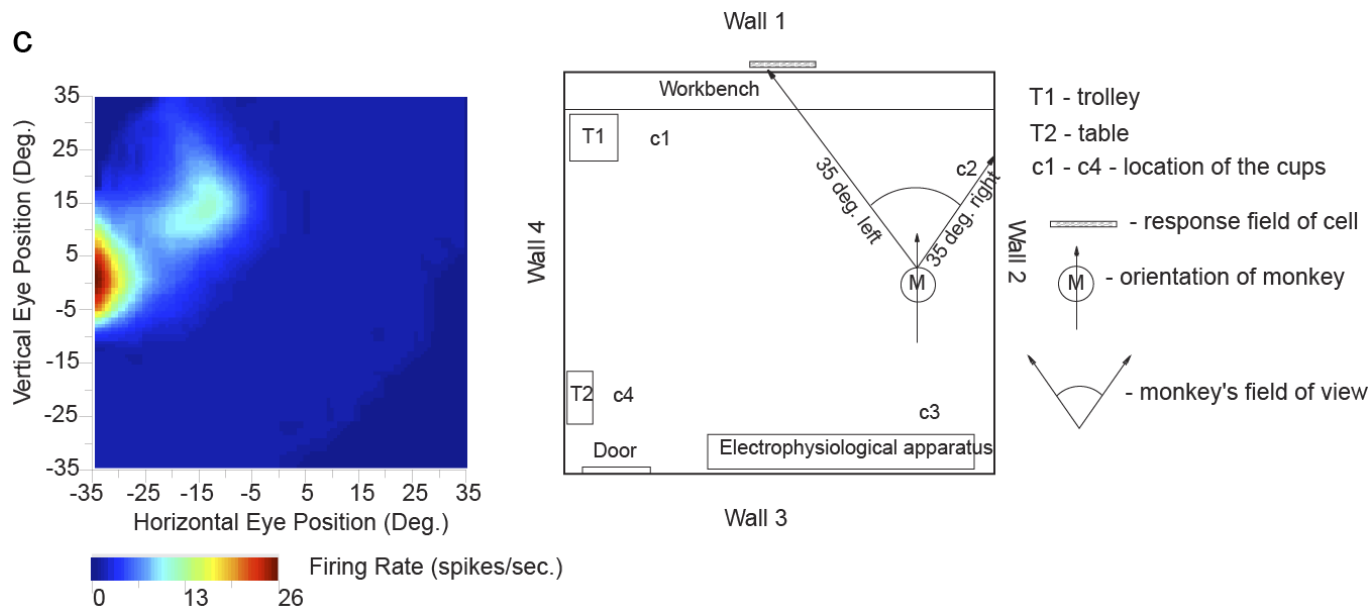
C

Figure 5c

Figure 5. (a)–(c) 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. Conventions as in Figure 3.

The responses of these spatial view cells have been shown to be independent of eye position, in that the cells respond provided that the effective part of allocentric space is being viewed. Of course, the eye position necessary for that part of space to be viewed (given the current coordinates of the head in the space) must be produced for the cell to respond. Indeed, the eye position/command signals are part of what does contribute to these cells responding (taking into account also the current head coordinates and place), in that most of the cells (apart from those in the CA3 field) respond only when the eyes are looking at the correct spatial field for the cell, even if the view details are obscured by curtains or darkness (Robertson *et al.*, 1998). In addition, we note that the evidence presented in this paper shows that the neurons do not respond in relation to eye movements *per se*, in that when the monkey is not looking towards a spatial view field, the neurons are either totally silent, or have a very low level of spontaneous activity, even though the monkey is making saccades. Evidence of this type is included in Figures 3e and 4b. Such evidence shows that eye movements *per se* do not cause these neurons to fire.

This allocentric type of spatial coding is very different from the egocentric encoding, relative to the head or body, found in the parietal cortex (see Stein, 1992; Andersen, 1995) in terms of the coordinate system being used. It is also different in terms of how the information is represented. Andersen and colleagues described a representation in which each cell responded to a combination of retinal position and eye position. An individual cell could thus code that a visual stimulus was at a given position in head-related space, but only for one combination of retinal position and eye position. Other cells were needed for the same position in head-related space when this corresponded to other combinations of position on the retina and eye position. In

contrast, in the representation described here in the hippocampal formation, a single cell does not code for only one of the possible combinations of head position plus direction, and eye position, which specify a particular location in (room-based) allocentric space. Instead, a single cell codes for a given position in allocentric space, whatever the head coordinates and eye position.

We note that this is an appropriate level of encoding for a representation in an associative memory, which must store, for example, where in space an object was seen. With the type of encoding described here, that part of space has a unique neural representation. This allows for economy of storage, in that the capacity of the memory is not taken up by having to remember an object together with an innumerable set of possible head/eye position combinations. It also simplifies generalization in the read-out from the memory, in that an external system does not have to decode all the different possible head/eye position combinations as corresponding to the same position in space. With the combination type of encoding, at recall the particular combination of head position/direction plus eye position might be correctly recalled from the object-place associative memory, but this would not generalize to the same position in allocentric space encoded by other possible head position/direction and eye position combinations. The outcome of these computational considerations is that probably the representation the hippocampus needs for its purposes is of allocentric position in space out there, and that is what is provided as shown by the results described here.

Given that the cells do not respond to head direction *per se*, or to eye position *per se*, the evidence that these cells respond to a position 'out there' in allocentric space is strengthened. [Further evidence that the spatial view cells are not head direction cells is
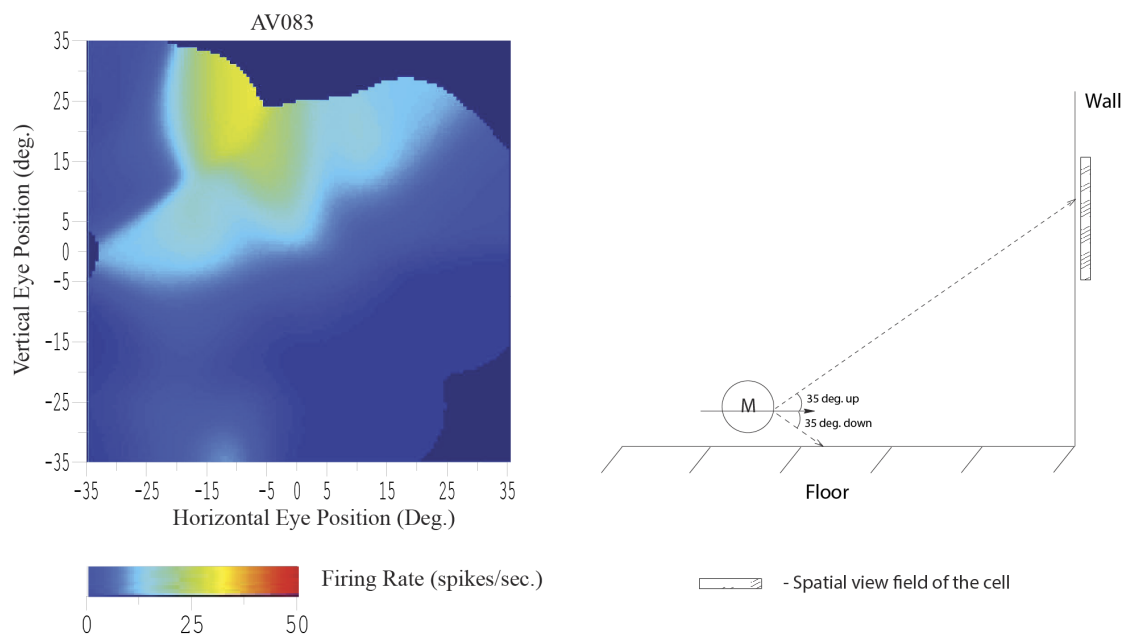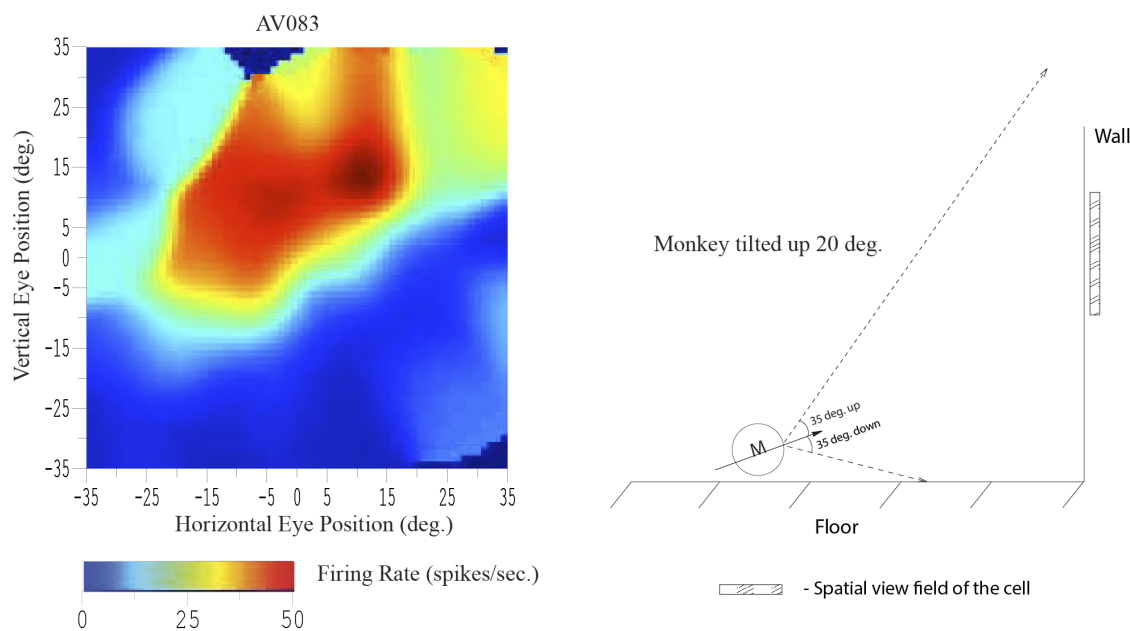
Figure 6*a*

Figure 6*b*

that we have recently found head direction cells, mainly in the monkey presubiculum, and their responses have been shown in the identical testing situation, in contrast, to be tuned to head direction, independently of the place where the monkey is located and of the spatial view that can be seen (see Rolls *et al.*, 1998b; Robertson *et al.*, 1999; head direction cells in rats are reviewed by Taube *et al.*, 1996).] The data shown in Figures 1–4 and Table 1 add to the previous evidence that it is not where the monkey is in space, but where he is looking in space, that determines whether these cells respond (Rolls *et al.*, 1997a,b;

Robertson *et al.*, 1998). The representation of allocentric space described here and in related studies (Rolls *et al.*, 1997a, 1998a,b; Robertson *et al.*, 1998) in the monkey which can locomote round an environment is, however, quite similar to that described in the hippocampus of the stationary monkey performing object–place memory tasks (Rolls *et al.*, 1989) in which the coordinates are also allocentric, in some cases in allocentric space relative to the screen, and in other cases in room-based space (Feigenbaum and Rolls, 1991).

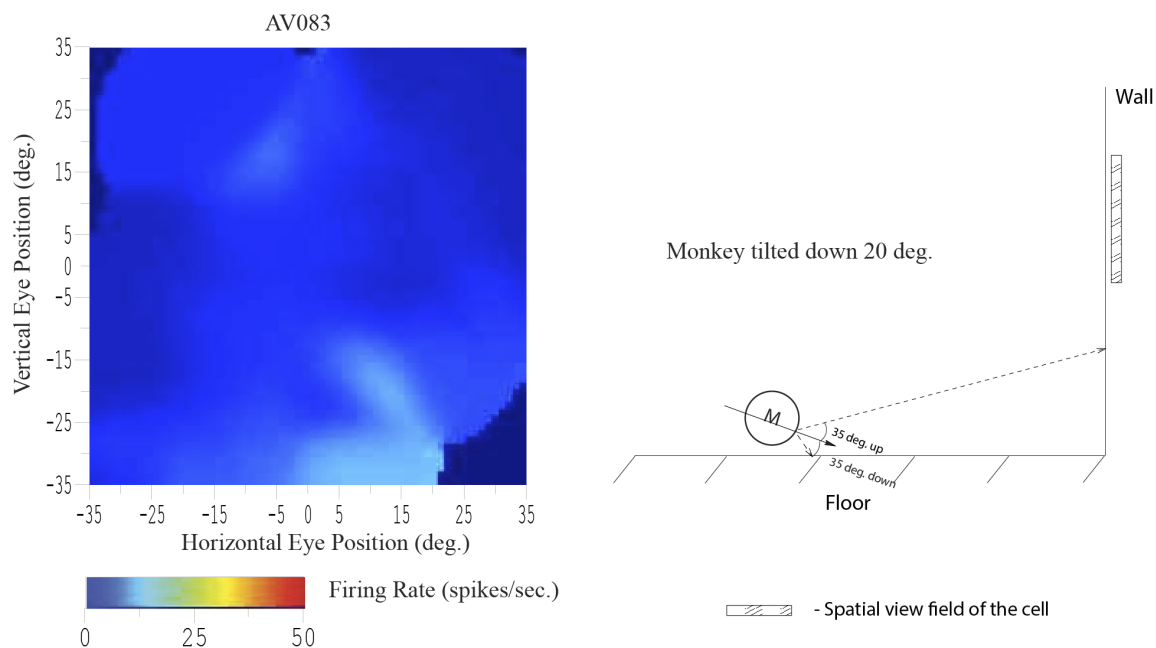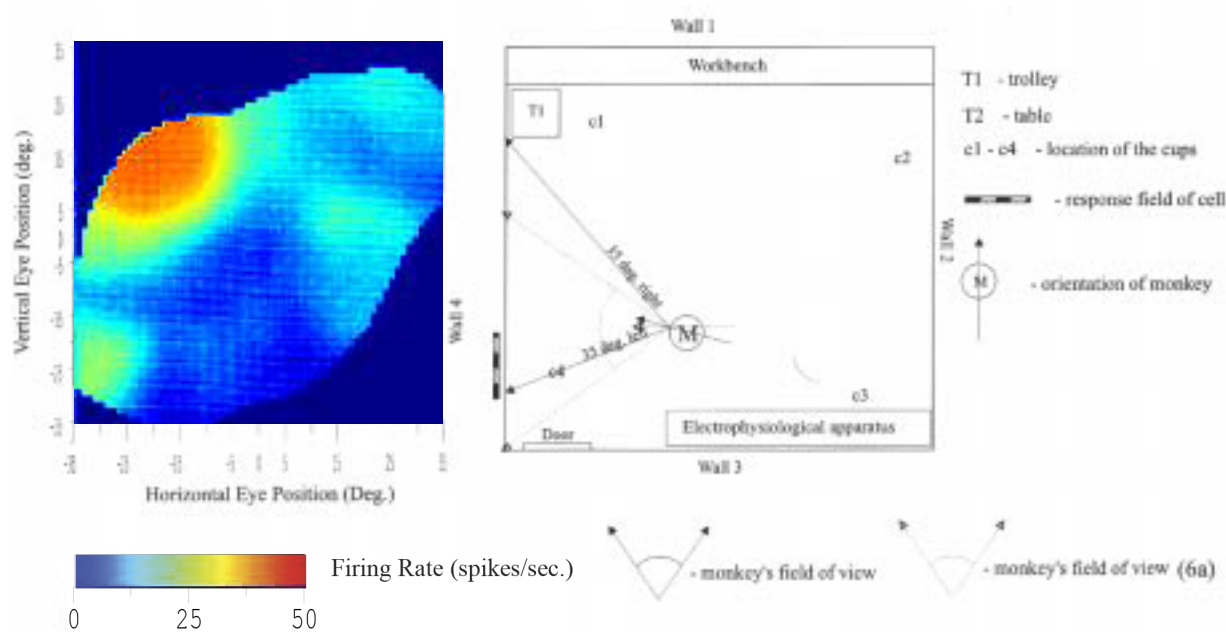The cells described here were typically searched for during

Figure 6c

Figure 6d

Figure 6. Examples of the firing of a hippocampal cell when the monkey was tilted to different head orientations with respect to the coronal plane (i.e. different pitches). The firing rate of the cell in spikes/s projected onto the wall of the room is indicated by the blackness of the diagram on the left (with the calibration bar in spikes/s shown below). (*a*) Head horizontal. (*b*) Head tilted up 20°. (*c*) Head tilted down 20°. (*d*) A horizontal shift of the spatial view field occurred to the monkey's left when the monkey was rotated clockwise to face in the direction indicated by the solid lines. The horizontal direction in which he was facing for (*a*)–(*c*) is shown by the dotted lines in (*d*). Conventions as in Figure 3.

active locomotion. If a cell had a spatial view field during active locomotion, the field could also be demonstrated with the monkey stationary, as shown, for example, in Figures 1–4 (see also Rolls *et al.*, 1997a, 1998a). It could, of course, be that experience with active locomotion in the environment helped the cells to respond with the monkey stationary. The possible

difference from findings in the rat (cf. Foster *et al.*, 1989) may be due to the fact that even a stationary monkey can actively explore its environment by precise eye movements. Indeed, primates can explore visual environments perfectly well and actively by the use of eye movements. We also note that the monkey was remarkably unrestrained in the recording situation

Table 1

The average information and maximum information I_{max} available from the responses of each cell about spatial view, eye position, head direction and place (the ANOVAs tested whether each cell had significantly different firing rates to different spatial views, eye positions, head directions and places). NA, not applicable

| Cell	Allocentric view					Eye position					Head direction					Place				
	Information (bits)	I_{max} (bits)	ANOVA			Information (bits)	I_{max} (bits)	ANOVA			Information (bits)	I_{max} (bits)	ANOVA			Information (bits)	I_{max} (bits)	ANOVA		
			F	(df)	P			F	(df)	P			F	(df)	P			F	(df)	P
av232c1	0.053	0.246	13.61	(7)	0.0001	0.004	0.008	3.696	(2)	0.025	0.002	0.003	0.006	(1)	0.937	0.066	0.095	2.14	(3)	0.093
av237c1	0.015	0.261	5.69	(2)	0.003	0.000	0.034	0.956	(11)	0.485	NA	NA	NA			0.005	0.008	0.530	(1)	0.467
az033c2	0.090	0.416	17.01	(7)	0.0001	0.005	0.150	1.629	(11)	0.085	0.012	0.040	1.895	(2)	0.151	0.000	0.001	0.461	(1)	0.497
az034c1	0.109	0.416	5.92	(7)	0.0001	0.013	0.014	2.371	(1)	0.125	0.006	0.007	0.520	(1)	0.471	0.005	0.007	0.528	(1)	0.468
az110c3	0.099	0.297	5.74	(7)	0.0001	0.000	0.003	0.024	(1)	0.877	0.001	0.007	0.895	(3)	0.443	0.007	0.019	2.464	(2)	0.085
Avg	0.073	0.327				0.004	0.042				0.005	0.014				0.017	0.026			
av057c1	0.617	1.077	39.4	(7)	0.0001	NA	NA	NA			NA	NA	NA			0.000	0.000	0.121	(2)	0.886
av071c4	0.934	1.074	29.2	(3)	0.0001	NA	NA	NA			0.217	1.034	5.25	(1)	0.038	0.165	0.218	0.535	(2)	0.59
av083c1	0.295	0.690	8.93	(10)	0.0001	0.028	0.117	1.88	(8)	0.088	NA	NA	NA			NA	NA	NA		
av102c1	0.236	0.499	7.15	(4)	0.0001	NA	NA	NA			0.000	0.000	0.14	(1)	0.72	0.000	0.148	1.334	(3)	0.277
av197c2	0.522	1.100	10.95	(3)	0.0001	NA	NA	NA			0.000	0.000	0.031	(1)	0.864	0.000	0.000	0.107	(1)	0.75
av216c2	0.217	0.433	4.66	(5)	0.001	0.006	0.111	0.35	(4)	0.84	0.000	0.001	0.454	(1)	0.501	0.000	0.005	0.02	(1)	0.889
Avg	0.470	0.812				0.017	0.114				0.054	0.259				0.033	0.074			
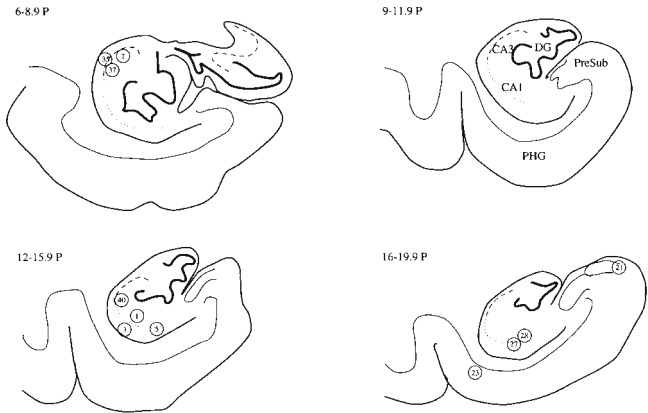
Figure 7. The hippocampal and parahippocampal sites at which different spatial view cells were recorded. Coronal sections at different distances in mm posterior (P) to the sphenoid reference are shown. The number inside each circle corresponds to the cell number shown in Table 2 in brackets. CA3, CA3 hippocampal pyramidal cell field; CA1, CA1 hippocampal pyramidal cell field; DG, dentate gyrus; PreSub, presubiculum; PHG, parahippocampal gyrus.

Figure 8. The hippocampal and parahippocampal sites at which different cells were recorded in this study, to show the regions sampled. Each circle marks the location where a cell was recorded. The figure shows the locations of 296 of the 354 cells recorded, with 58 not shown in the diagram because they were close to other cells plotted. The filled circles are from monkey az, and the open circles from monkey av. Coronal sections at different distances in mm posterior (P) to the sphenoid reference are shown. Labels as in Figure 7.

during active locomotion while the response of a spatial view cell was being first characterized, in that it could run round the environment with velocities as great as 0.6 m/s, and could move its head with angular velocities as great as 100°/s (see Rolls *et al.*, 1997a, 1998a).

Many view (or 'space' or 'spatial view') cells have been found in this series of experiments in the locomoting monkey (Rolls *et al.*, 1997a, 1998a; Robertson *et al.*, 1998). 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) 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 in this paper is generally needed to show that a cell in the primate hippocampus responded to the place where the monkey was rather than spatial view. One issue is that a region of allocentric space in a room which defines the spatial view field of a spatial view cell
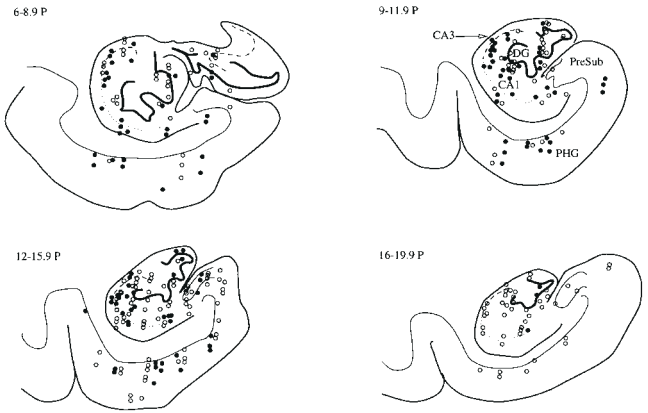
may not be visible from all places in a room. For example, if the monkey was at the place of the door shown in Figure 3, it could not see the spatial view which included cup 3 (c3), because of the apparatus shown. It is therefore in general not sufficient to show that the firing rate depends on the place where the monkey is, because the spatial view may as well. This point 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.

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. The spatial view cells described in this and related papers (Rolls *et al.*, 1997a, 1998a; Robertson *et al.*, 1998) in primates would be useful as part of a memory system, in that they would provide a representation of a part of

Table 2
Properties of the spatial view cells

Cell no.	Field	Peak rate (sp/s)	Spont. rate (sp/s)	Location	Recording time (min)
av057 (1)	corner 3	18.9	0.9	CA1	25
av071 (3)	corner 3/4	16.2	0.6	CA1	18
av083 (5)	wall 4	19	2.1	CA1	12
av102 (7)	corner 4	43.5	0.4	CA3	20
av197 (21)	wall 4	16.5	1.7	PSUB	10
av216 (23)	wall 1	13.2	0.4	PHG	16
av232 (27)	corner 1	4	0.2	CA1	68
av237 (28)	wall 4	7.5	0	CA1	43
az033 (35)	wall 3	21	0	CA3	97
az034 (37)	corner 4	25.5	0	CA3	36
az110 (40)	wall 3	14.25	0.35	CA3	35

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, all examples of episodic memories. We have suggested elsewhere that such episodic memories could be laid down in the hippocampus using the neuronal network process of association, implemented by the recurrent collateral axons of the CA3 neurons (see Rolls, 1989, 1996; Treves and Rolls, 1994; Rolls and Treves, 1998). The spatial view cells described here would be well suited to provide the spatial representation required for such a memory function, in that they respond to a spatial location being looked at in allocentric coordinates. In other experiments we have shown that there are indeed also in the hippocampal formation some neurons that respond only to objects in certain allocentrically defined locations (Rolls *et al.*, 1989; Feigenbaum and Rolls, 1991). Further evidence relating the spatial view cells in the hippocampus to a function in memory is that some can still respond, though at a reduced rate and with some drift of the spatial view field, when the monkey looks towards a spatial location that is no longer visible (Robertson *et al.*, 1998). It is found that the proportion of cells in the primate hippocampal formation that responds to spatial view is substantial (40/352 cells, or 11.4%; see Rolls *et al.*, 1997a, 1998a). We note that almost all the recording was performed in one room, which provided only a small proportion of all the spatial views known to the monkeys. It may be that by not allocating a very high proportion of cells to be spatial view cells for a single room, other cells may be available to encode spatial views of the wide range of environments that monkeys normally process. In addition, it is known that other cells in the primate hippocampal formation code for whole body motion (O'Mara *et al.*, 1994), for remembering (Cahusac *et al.*, 1989) and for learning (Miyashita *et al.*, 1989) spatial responses, and for object–place memory (Rolls *et al.*, 1989; see Rolls, 1999).

The representation of space in the rat hippocampus, which is of the place where the rat is (O'Keefe and Nadel, 1978; O'Keefe, 1991; Burgess *et al.*, 1994; Muller *et al.*, 1994; Markus *et al.*, 1995), is compared to that found in the primate hippocampus elsewhere (Rolls *et al.*, 1997a, 1998a; Rolls, 1999; Robertson *et al.*, 1998). In primates, and possibly also in rats, the neuronal representation of space in the primate hippocampus may be appropriate for forming memories of events (which usually have a spatial component). 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. We note in any case that representing space for spatial functions such as spatial navigation and computation implies the ability to store representations of spatial environments which have been seen and to recall them.

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