A View Model Which Accounts for the Spatial Fields of Hippocampal Primate Spatial View Cells and Rat Place Cells

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ABSTRACT: Hippocampal spatial view cells found in primates respond to a region of visual space being looked at, relatively independently of where the monkey is located. Rat place cells have responses which depend on where the rat is located. We investigate the hypothesis that in both types of animal, hippocampal cells respond to a combination of visual cues in the correct spatial relation to each other. In rats, which have a wide visual field, such a combination might define a place. In primates, including humans, which have a much smaller visual field and a fovea which is directed towards a part of the environment, the same mechanism might lead to spatial view cells. A computational model in which the neurons become organized by learning to respond to a combination of a small number of visual cues spread within an angle of a 30° receptive field resulted in cells with visual properties like those of primate spatial view cells. The same model, but operating with a receptive field of 270°, produced cells with visual properties like those of rat place cells. Thus a common hippocampal mechanism operating with different visual receptive field sizes could account for some of the visual properties of both place cells in rodents and spatial view cells in primates. *Hippocampus 2001;11:699–706.* © 2001 Wiley-Liss, Inc.

INTRODUCTION

It has been demonstrated that rat hippocampal pyramidal cells respond when the animal is located at a particular place in a given environment, and these cells are designated as place cells (O'Keefe and Dostrovsky, 1971; McNaughton et al., 1983; O'Keefe, 1984; Muller et al., 1991, 1994; Markus et al., 1995; O'Keefe et al., 1998). This observation, together with the fact that lesions in the hippocampus impair navigation based on allocentric visual cues, led to the cognitive map theory of the hippocampus (O'Keefe and Nadel, 1978; Redish, 1999). This hypothesis raises the question of exactly how visual cues influence hippocampal cells in rats to result in their firing when the rat is at a particular place in a visual environment.

In contrast, in recordings made in the primate hippocampus during spatial tasks including active walking in a spatial environment, Rolls et al. found little evidence for place cells, but have discovered that there are *spatial view cells.* These cells respond when the monkey is looking at particular places in the environment, and their firing is relatively independent of the place where the monkey is located (Rolls et al., 1997, 1998; Georges-François et al., 1999; Robertson et al., 1998; Rolls, 1999). The representation of space that they provide is in allocentric coordinates (Georges-François et al., 1999; Rolls et al., 1998; Rolls, 1999). Many spatial view cells continue to fire in the dark when the monkey looks towards the spatial view field, and indeed the representation is updated by idiothetic (self-motion) cues such as eye position and head direction (Robertson et al., 1998). The activity is maintained by an ongoing memory process, in that the spatial view field can show some drift in darkness, and may last for only a number of minutes. In addition, a small proportion of primate spatial view cells are task-dependent, in that in an object-place memory task, the responses of some depend on not only the spatial position of the stimuli, but also on whether the object has been shown in that location before, the task being performed by the monkey (Feigenbaum and Rolls, 1991). In these respects, spatial view cells in primates are analogous to place cells in rats. The difference is that rat place cells represent the place where the rat is located, and primate spatial view cells represent the place at which the monkey is looking (Rolls, 1999).

In this paper we consider whether a common hippocampal mechanism could lead to place cells in rodents and spatial view cells in primates. If visual cues in the environment are to play a role in producing these types of neuronal response, then the size of the field of view is likely to be an important parameter. For example, in the case of the rat which has a large field of view (180–270°; see Rolls, 1999; Walls, 1967; Duke-Elder, 1958; Adams and Forrester, 1968), hippocampal cells which responded to a combination of visual cues present in this wide field of view in a given relative spatial relation might encode the place where the rat was located (see Fig. 1a).[1] In contrast, in the case of primates (including humans),

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[1]These values for the field of view of rats are arrived at by noting that the rat retina subtends 150° in the visual field (Walls, 1967), and that the optic axis of the rat eye is oriented at 60° from the body axis (Duke-Elder, 1958), producing an estimated field of view of 270°; and also by direct recording of visual-evoked potentials in the rat

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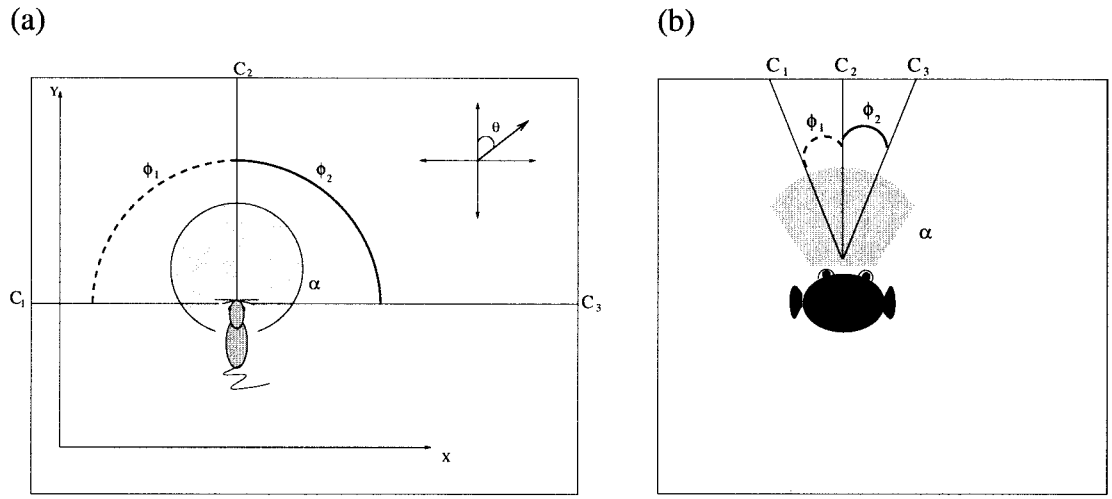

FIGURE 1. Sketch of square containment area in which the agent is situated. The containment area contains a grid of 200 × 200 possible positions *x*, *y* which the agent visits during the simulations, and at each position the agent rotates its head direction θ through 360° in increments of 5°. In addition, the containment area has a number of visual cues distributed evenly around the perimeter. As the agent explores its environment, individual hippocampal cells are stimulated by specific visual cues currently within the field of view of the agent α. Left: The case for a rat with a 270° field of view. Right: The case for a primate with a 30° field of view. Shaded areas correspond to sizes of fields of view of agents. In the model presented here, the firing rates of hippocampal cells are dependent on angles ϕ subtended by visual cues currently within the field of view of the agent.

partly because of the foveate nature of the retina, a relatively small portion of space (20–30°) is usually viewed at one time, and if hippocampal neurons respond to a combination of visual cues towards which the animal's gaze was directed, then this might produce spatial view cells (see Fig. 1b).[2] An underlying conceptualization is that hippocampal cells learn to respond to a combination of landmarks present together at the same time within the visual field. If the visual field is large, then this type of learned combination will lead to place fields. On the other hand, if the field visible at any one time is small, as in primates, then the combination of landmarks that can be associated together by associative (Hebbian) learning will cover a small area of visual space, and the neuron will thus have responses like those of a primate spatial view cell.

To investigate the relationship between the responses of rat place cells and primate spatial view cells, we formulated a model to investigate how differences in the field of view of rodents and primates might lead to differences in the spatial response properties of their hippocampal cells. During simulations of the model, the agent was allowed to explore a given environment, and the effects of altering only the size of the field of view (α in Fig. 1) were investigated. In principle, place fields can be determined in several ways (e.g., McNaughton et al., 1996; Burgess and O'Keefe, 1996). A simple geometric model is described here. It is based on the local view subsystem of the agent (Zipser, 1985; Leonard and McNaughton, 1990; Touretzky and Redish, 1996; Redish, 1999), in the sense that the neuronal responses are determined by the visual sensory aspects of environmental landmarks. Our model uses what we call an "angles subtended" approach. The underlying hypothesis is that the responses of hippocampal neurons are determined by calculating the angles subtended between sets of visual cues distributed across the environment. The basic parameters of the model are the number of visual cues within the field of view and the angles subtended between them with respect to the agent. It should be noted that the distance between the agent and the visual cues is not an explicit parameter used in calculations.

The results of the simulations show that the model is able to produce either place or spatial view cells, depending on the size of the field of view of the agent. This suggests that the hippocampus and its input systems could use similar mechanisms to determine the spatial response properties of its cells, with the differences in neuronal responses being at least partly due to the different sizes of the visual fields of rats and primates. Moreover, the results suggest that a mechanism analogous to that which could lead to the spatial view cells found in primates could be involved in generating the visual response properties of place cells in rodents.

visual cortex produced by stimuli at different positions in the visual field (Adams and Forrester, 1968).

[2]The foveate nature of the primate retina results in acuity declining markedly from its foveal value by 15° away from the fovea in humans, and in macaques the decline is likely to be greater due to the reduction in retinal ganglion cell density and the cortical magnification factor (Wilson et al., 1990; Rolls and Cowey, 1970).

THE MODEL

In the model, each cell fires maximally when the angles subtended by visual cues in the current field of view of the agent are close to those that were learned by the cell when the agent was in a given position in the environment with a given head direction,

producing what was defined for that cell as its optimal view. However, consistent with neurophysiological observations (O'Keefe and Speakman, 1987), we assume that not all of the cues associated with the optimal view need to be within the field of view of the agent for the cell to be stimulated, and that the cell can be activated by a subset of the cues from the original optimal view which are present in the current field of view, provided that they subtend the correct angles with respect to each other. Specifically, in the model presented here, the cell will be stimulated if there are at least three cues present from the optimal view. This is because at least three cues are required within the field of view of the agent to uniquely specify the location of the agent within a plane. If we consider the case of a rat with a large field of view, say 270°, then the optimal view for a particular cell will encompass visual cues in a 270° arc around the animal. Whatever the head direction, it is likely that more than three cues from the optimal environmental view will always lie within the field of view of the animal. Then, as long as the animal remains in the location associated with the optimal view, the angles subtended by the visible cues will be close to the ideal angles associated with the optimal view. Thus, in this case the cell will appear to fire when the animal is at a particular location. However, if we consider the case of a primate with a relatively small field of view, say 30°, then the optimal view for a particular cell will encompass visual cues in a 30° arc ahead of the animal. This means that all of the cues associated with the optimal view will occur in a particular spatial location towards which the primate is looking. In this case, the cell will fire maximally when the animal is looking at the appropriate location in space.

The details of the model are as follows. An agent is placed into a square environment (containment area) at a location (x, y) with a head direction θ, as shown in Figure 1. The containment area contains a grid of 200×200 possible positions which the agent visits during the simulations, and at each position the agent rotates its head direction through 360° in increments of 5°. The containment area has a number of visual cues distributed evenly around the perimeter. Then, an optimal view is randomly assigned to a cell in the model by choosing an arbitrary location $(x_{\text{ideal}}, y_{\text{ideal}})$ and head direction θ_{ideal} for the agent. When the agent is so positioned, the visual cues will have the correct arrangement with respect to the agent to stimulate the cell maximally. Then, given the field of view α of the agent, the location $(x_{\text{ideal}}, y_{\text{ideal}})$ and head direction θ_{ideal} define which visual cues are within the optimal view, and define the ideal angles subtended by these cues with respect to the agent for which the cell fires maximally. That is, with the agent located at $(x_{\text{ideal}}, y_{\text{ideal}})$ with a head direction θ_{ideal}, for each pair of cues (c_1, c_2) within the field of view α of the agent, the ideal angle $\phi_{\text{ideal}}^{(c_1, c_2)}$ subtended by the cues with respect to the agent is calculated and stored. Once the cell has been assigned an optimal view and the ideal angles $\phi_{\text{ideal}}^{(c_1, c_2)}$ have been calculated, the firing rate of the relevant cell with the agent situated at any new location and head direction is calculated as follows. First, given the current location (x, y) and head direction θ of the agent, the number of cues from the original optimal view that are within the current field of view α of the agent is calculated. If there are less than three cues, then the firing rate $r_{(x,y)}^{\theta}$ of the cell for location (x, y) and head direction θ is set to zero. If there are three or more cues, then the calculation proceeds as follows. For each pair of cues (c_1, c_2) within the current field of view of the agent, the actual angle $\phi(c_1, c_2, x, y)$ subtended by the cues with respect to the current (x, y) location of the agent is calculated. Then for each pair of cues (c_1, c_2), the following difference between the actual and ideal angles is calculated

$$e_{(x,y)}^{(c_1,c_2)} = |\phi(c_1, c_2, x, y) - \phi_{\text{ideal}}^{(c_1,c_2)}|. \tag{1}$$

In Equation (1), the absolute value of the difference between the actual and ideal angles is calculated. However, although not implemented in the simulations presented here, an alternative step might be to calculate a Gaussian of this difference. The same operation is performed for a number of pairs of cues (typically 10 in the simulations, as described in Results) within the field of view α, excepting repeated pairs of the form $(c_1, c_2) = (c_2, c_1)$. Then the average difference between the actual and ideal angles for the pairs of cues is calculated as

$$E_{x,y} = \frac{\sum_{\{i,j\}} e_{(x,y)}^{(c_i,c_j)}}{N} \tag{2}$$

where $\{i, j\}$ denotes the set of the visible pairs of cues for which the cell responds to the angle subtended between the cues, and N is the number of such pairs of cues. A relatively small number of 10 for N was chosen for most simulations, on the assumption that each cell might not respond to a vast number of angular differences. In practice, we explored values for N in the range 6–32, and obtained similar generic results to those shown in the paper. Finally, the cell firing rate $r_{(x,y)}^{\theta}$ for position (x, y) and head direction θ is given by

$$r_{(x,y)}^{\theta} = \frac{\alpha - E_{x,y}}{\alpha}. \tag{3}$$

Since the terms $e_{(x,y)}^{(c_1,c_2)}$ must be less than the size of the field of view α, $E_{x,y}$ must also be less than α. Therefore, the effect of Equation (3) is to normalize the firing rates between 0 and 1. However, a mechanism that was found to be important for replicating the desired cell response properties was to include a tolerance T (with units in degrees) that ensures that all of the cue pairs must be close to the ideal angle before the cell fires. That is, if there is a cue pair (c_1, c_2) such that

$$|\phi(c_1, c_2, x, y) - \phi_{\text{ideal}}^{(c_1,c_2)}| \geq T \tag{4}$$

then we set $r_{(x,y)}^{\theta} = 0$. This mechanism should be similar in operation to calculating a Gaussian of the differences between the actual and ideal angles in Equation (1), as discussed above, but where the Gaussian profile is quite narrow.

In the simulations, place fields within the containment area, and spatial view fields around the perimeter of the containment area, are calculated as follows. During the simulation, the agent is moved through all 200×200 possible grid positions within the containment area, and in each position the agent has its head direction rotated through 360° in increments of 5°. For each head direction, the firing rate of the neuron is calculated as described above. To calculate place fields, for each location within the containment area the average firing rate of the cell is computed over all

head directions. The average cell firing rate in position (x, y) is given by

$$R_{(x,y)} = \frac{\sum_{\theta} r^{\theta}_{(x,y)}}{H} \quad (5)$$

where the sum is over all head directions of the agent, and H is the number of head directions of the agent. The above average is calculated for every position within the containment area. To calculate spatial view fields, the perimeter of the containment area is divided into a large number of small intervals or bins in which average firing rates are computed. Then, for each bin around the perimeter of the containment area, the average firing rate of the cell is computed over all instances in which a straight line along the agent's head direction fell into that bin. The average cell firing rate in a bin b on the perimeter is given by

$$R_b = \frac{\sum_{\Omega} r^{\theta}_{(x,y)}}{N_b} \quad (6)$$

where the sum is taken over the set Ω of all positions of the agent during the simulation defined by the triples x, y, θ for which a straight line along the agent's head direction fell into bin b, and N_b is the number of such positions. The number of visual cues that occupied the optimal field of view of the agent was a parameter of model, that was normally set to be eight cues, for both the rat and monkey simulations. However, we explored different values for the number of visual cues that activated a cell during initial training in the range 5–32, and found that the results were generically similar, as noted in Results. This parameter effectively represents how many cues in the initial training environment are actually used by each spatial cell, rather than the actual density of cues that might be available in natural environments. The actual density of cues in an environment is not strictly relevant to the model, as the cells of the model learn a defined number of visual cues during initial training in the environment.

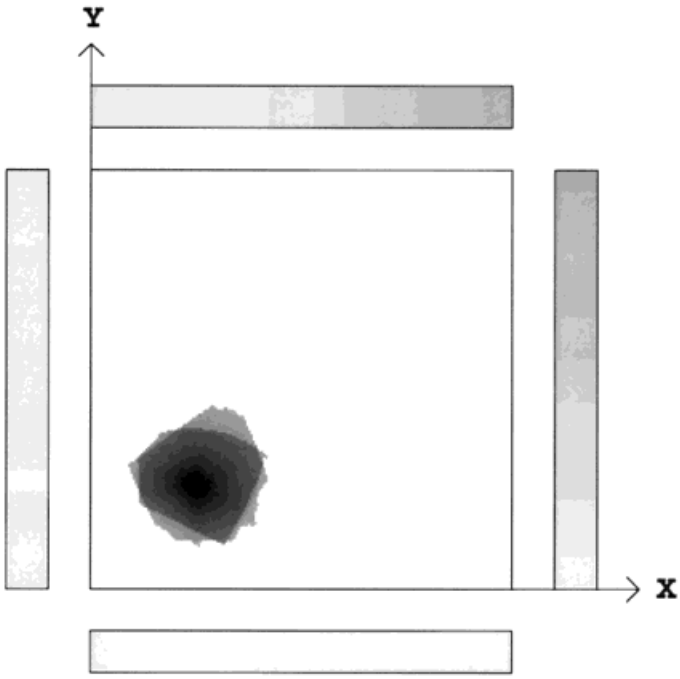

FIGURE 2. Simulation of cell firing, as an agent with a 270° field of view explored the containment area with sides of unit length. In the plot, the darkness of the shading is proportional to the average cell firing rate at that location, with high firing rates signified by black and low firing by white. Within the containment area are plotted the average firing rates of the cell when the agent was at particular locations, and these plots show a place field centered at $(x_{ideal}, y_{ideal}) = (0.25, 0.25)$. Around the perimeter of the containment area are plotted the average firing rates of the cell when the agent was looking at particular locations on the walls, and it is shown that there was low firing in every spatial view. In this simulation, the tolerance T was set to 40.

RESULTS

The simulations showed that in the model, the cells had place fields when the field of view is 270°, and had spatial view fields when the field of view was reduced to 30°–60°.

An example of a place field effect obtained is shown in Figure 2. The field of view α was 270°. In this case, eight cues within the optimal field of view in the environment were learned by the cells, and the tolerance was set to $T = 40$. Here, as in the following examples, $(x_{ideal}, y_{ideal}) = (0.25, 0.25)$, and $\theta_{ideal} = 270°$. The place field was well-defined, occupying approximately 15% of the containment area. Figure 2 also shows the spatial view field of the cell, which was very extensive, in that the cell responded when the agent was looking at all four walls of the environment. In this and all other Figures in this paper, during learning there was a constraint applied for biological plausibility that each cell should learn about only a relatively small number, 10, of angles ϕ between cues. We note that the model works just as well when each cell can learn about many more angles. If each cell can learn about only a few angles (e.g., $\leq$10), then clearly angles between cues in the same small sector of space cannot provide sufficient spatial information, and in this situation the model was constrained to learn about nonadjacent pairs of cues in the environment.

The effects of increasing the tolerance to $T = 60°$ (but leaving the other parameters the same as in Fig. 2) are shown in Figure 3. The result is an increase in the absolute size of the place field, since a larger difference with respect to the ideal angle subtended is allowed. This results in more locations within the containment area being included in the place field. The opposite effects were found if the tolerance T was decreased (e.g., to 20, not illustrated).

The effects of decreasing the field of view α from 270° to 30° are shown in Figure 4. The tolerance used was as in Figure 2 (i.e., tolerance T was set to 40). The cells now had clearly defined spatial view fields (which occupied, as illustrated in Fig. 4, approximately half to one wall of the room). At the same time, the cells did not have clearly defined place fields (as illustrated in Fig. 4), in that they would respond when the agent was at almost all places in the

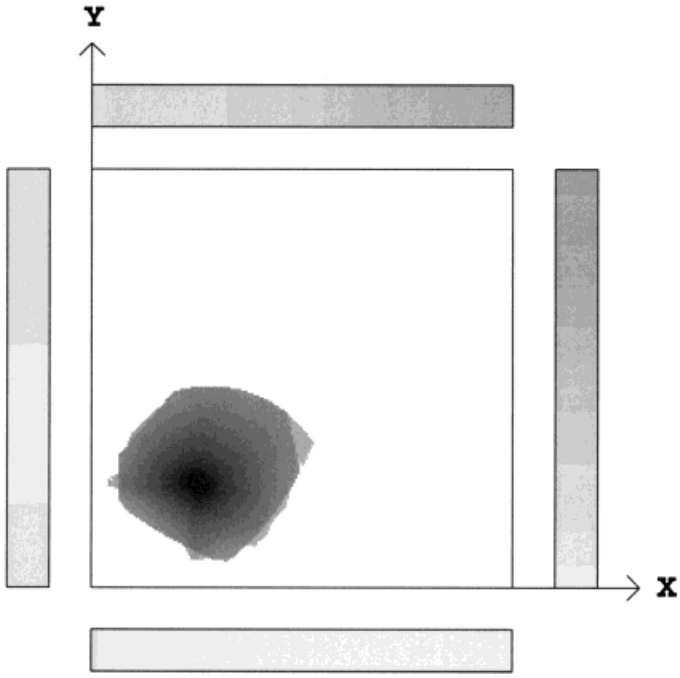

FIGURE 3. Simulation of cell firing, as an agent with a 270° field of view explored the containment area. This simulation is similar to that shown in Figure 2, except that here the tolerance *T* is increased to 60. The increased size of the tolerance *T* leads to a larger place field.

environment, provided that the agent was looking at the correct spatial view.

The effects with small visual fields of the agent (30°) of increasing the tolerance T to a value corresponding to that used in Figure 3 were negligible (because the angles subtended by the visible cues were always less than the 30° field of view), and this is not illustrated. The effect of decreasing the tolerance T was to decrease the size of the spatial view field to be smaller than that shown in Figure 4.

This model is not very sensitive to the actual distance of the agent from the spatial cues in the case where α is small (30°). This was shown in simulations in which the agent was restricted during testing to one or the other half of the environment in such a way that at testing, only near or only far cues could be used. The nature of the spatial view fields was little affected by this.

The plausibility of having a common computational hippocampal mechanism for spatial view and place fields modulated by the size of the field of view can be illustrated parametrically by analyzing the size of the place and spatial view fields with respect to the ratio between tolerance values T and size of the field of view α. For cases where eight cues were learned by a cell and the fields of view were 270° and 30°, the results are shown in Figure 5. The size of the spatial fields is plotted as a function of the relative tolerance of the angle computation process, which is simply the ratio of the tolerance parameter T of the model to the size of the field of view α in the model. Use of this ratio for the abscissa allows a direct comparison between the results from the model when using the value for α of 270° used for the rat simulations and the value of α of 30° used for the primate simulations. The curves at left in Figure 5 show for the fixed field of view of 30° (the primate case) that the spatial view fields remain well-defined and occupy a small proportion of the walls of the room, and at the same time the place fields occupy most of the environment for a wide range of values of the tolerance ratio. In contrast, the curves at right (Fig. 5) show for the fixed field of view of 270° (the rat case) that the place fields remain well-defined and occupy a small proportion of the environment, and at the same time the spatial view fields occupy most of the walls of the environment for a wide range of values of the tolerance ratio. For these graphs, the size of the spatial view fields was measured by the proportion of the walls for which the cell had an average firing rate greater than 0.2. Correspondingly, the size of the place fields was measured by the proportion of the containment area for which the cell had an average firing rate greater than 0.2. The results shown in Figure 5 thus show that the main factor that influences whether the cells become spatial view cells or place cells is the size of the visual field of the agent.

DISCUSSION

An important property of this model is that the cells change from having place fields into having spatial view fields if the field of view of the agent is reduced (from ≈270° to ≈30°). This property shows that an important factor in producing place cells in rodents

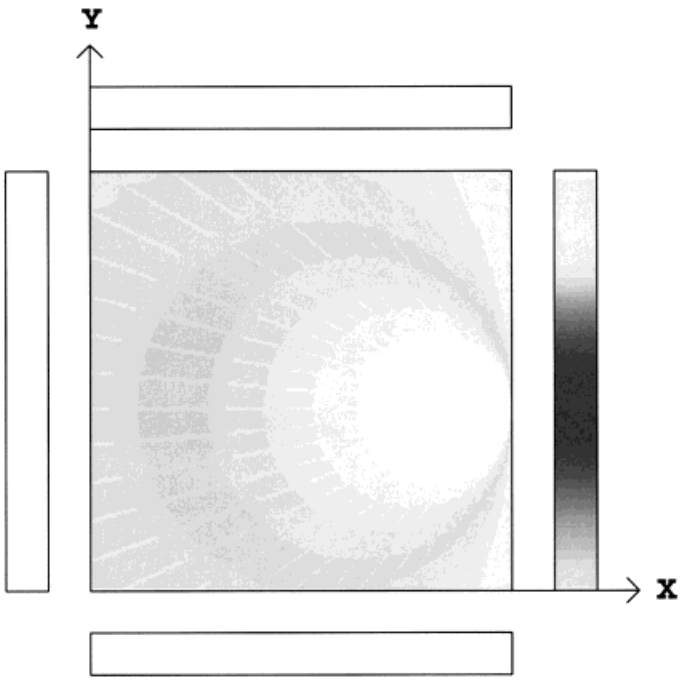

FIGURE 4. Simulation of cell firing, as an agent with a 30° field of view explored the containment area. Average firing rates plotted within the containment area show rather uniform firing for wherever the agent was located, while average firing rates plotted around the perimeter of the containment area show a well-defined spatial view field typical of those observed in neurophysiological studies with primates. In this simulation, the tolerance *T* was set to 40.

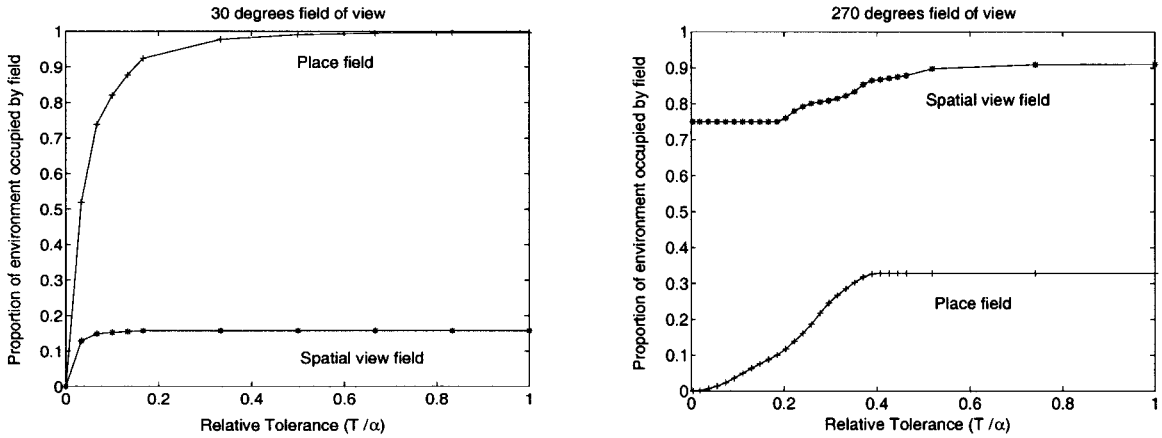

FIGURE 5. Size of spatial fields is plotted as a function of the relative tolerance of the angle computation process, which is the ratio of tolerance parameter *T* of the model to the size of the field of view α in the model. Left: Field of view of the agent = 30°, the "primate case." Right: Field of view of the agent = 270°, the "rat case."

(which have large visual fields) and spatial view cells in primates (which see a smaller field of view at any one time) could be the size of the visual fields, as proposed by Rolls (1999), and tested quantitatively by numerical simulation as described in this paper. The property arises in a model in which the response properties of hippocampal cells are set up by a learning mechanism, in which cells learn to respond to a spatial combination of landmarks visible together at any one time in the environment. Thus a common and generic process operating within the hippocampus and its input systems could operate to produce cells with spatial firing produced by visual cues that could account for hippocampal place cells in rodents and spatial view cells in primates.

The model used only the angles subtended by landmark cues in the environment. There was no explicit encoding of the distance between the agent and the visual cues. Although distance from the cues has been used in some previous models of hippocampal spatial cells (Burgess and O'Keefe, 1996) and not in others (McNaughton et al., 1996), we did not use distance as part of what determines the responses of cells. The reasons for this are that in primates, spatial view cells are little affected by the distance from the landmark cues (Rolls, 1999); and that there is not strong evidence that this is explicitly encoded by hippocampal cells in rats. We note that the conclusion from the investigations described here is that the size of the visual field may have a large effect on the response properties of neurons involved in spatial functions, even if the detailed explanation of the factors that account for the response properties of hippocampal spatial cells includes a number of other factors.

Predictions one might make from the hypotheses developed here are that it might be possible to influence the spatial representations found in the hippocampus by altering the extent of the field of view. For example, it is possible that the responses of rat place cells might become more like those of primate hippocampal spatial view cells if the rats had a less extensive view of the visual world.

These ideas lead to the more general conclusion that the representation of spatial knowledge in both rats and monkeys is such that it is convenient for the formation of episodic memories (Rolls, 1999). In particular, the representation of place in rats would be appropriate for associating an object with a given place at which the rat was located, such as a submerged platform in a particular place. The finding that some rat hippocampal neurons reflect more than the place where the rat is located is consistent with the possibility that rat hippocampal neurons are involved in a memory process (Wiener et al., 1989; Otto and Eichenbaum, 1992; Hampson et al., 1999; Eichenbaum and Harris, 2000; Kali and Dayan, 2000) (which might correspond to episodic memory in nonhuman primates and humans). Correspondingly, in primates, spatial view cells would be useful for storing an episodic memory that a particular object was at a particular seen place in the environment (Rolls et al., 1989; Miyashita et al., 1989; Feigenbaum and Rolls, 1991; Rolls, 1999). With spatial view cells, the place of the object or person in an environment could be remembered even if the viewer was not at that place. (This is because the spatial view cell firing that represents the place "out there" in an environment where an object is being seen could be associated with a representation of the object, to form an "object-place" memory, which is prototypical for event or episodic memory; Rolls, 1999.) This type of memory is a frequent everyday occurrence in primates including humans, and could not be performed by place cells (Rolls, 1999). (Place cells could not implement this, as they do not fire unless the organism is actually at the place in question.) The mechanism would involve associative synaptic modification in an autoassociative network between a representation of a place (in rats) or of a viewed place (in primates) present in the hippocampus, and a representation of an object (Rolls, 1999; Rolls and Treves, 1998; Treves and Rolls, 1994).[3] It is of interest that it is exactly the same type of associative mechanism that could underlie the formation of spatial view and

[3]We note that the hypothesis that CA3 is an autoassociative network useful for episodic memory was related to ideas of Marr (1971) (who did not name the CA3 region), was developed by Gardner-Medwin (1976), was specified more formally by Rolls (1987) and McNaughton and Morris (1987), and was developed analytically by Treves and Rolls (1992, 1994). This theory was recently reviewed by Redish (1999), but not in the context of

place cells in the model described here, namely, associative synaptic modification between representations of landmark cues in the environment. Thus a single type of associative process which could even be implemented in a single brain network could underlie the formation of episodic memories and the representation of places in an environment. In this way, memories useful for spatial navigation and episodic memories of particular object locations could be products of a general mechanism responsible for the storage and recall of information about a particular set of events which occur together at the same time. A possible implementation of this is close to current models of hippocampal function, where associative learning between CA3 pyramidal cells plays a central role, along with competitive learning in the dentate gyrus, which sharpens up the representations first (Rolls, 1999; Rolls and Treves, 1998; Treves and Rolls, 1992, 1994).[4]

Finally, we note that if spatial information, such as a place or a spatial view, is to be stored in a network, then because space is inherently continuous, a continuous attractor network may be needed (Amari, 1977; Zhang, 1996; Samsonovich and McNaughton, 1997; Stringer et al., 2001a,b,c). Such a network can maintain a packet of neuronal firing after the initiating stimulus is removed, and this property usefully models the maintenance of firing in the dark of place cells (Quirk et al., 1990; Markus et al., 1994), head direction cells (Taube et al., 1996; Muller et al., 1996; Robertson et al., 1999), and spatial view cells (Robertson et al., 1998). In addition, idiothetic (self-motion) cues (such as body movement) can update in the dark (and probably in the light) the spatial representations provided by place cells (Quirk et al., 1990; Markus et al., 1994), head direction cells (Taube et al., 1996; Muller et al., 1996; Robertson et al., 1999), and spatial view cells (Robertson et al., 1998), providing evidence that nonvisual cues as well as local view inputs can update the firing of these spatial representations. In considering how this update by idiothetic cues could occur, Skaggs et al. (1995) suggested a process by which idiothetic neuronal firing could drive the activity packet, but not a mechanism for the synaptic weights from the idiothetic inputs to be set up; Zhang (1996) suggested that the weights in the continuous attractor might be dynamically modified by the idiothetic cues but provided no mechanisms; Samsonovich and McNaughton (1997) suggested a method that uses what is essentially a look-up table; and Stringer et al. (2001a,b,c) proposed how the appropriate connections for performing the idiothetic update of the continuous attractor could be set up by self-organizing learning.

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primates remembering where objects are in space "out there," i.e., where the eyes are looking.

[4]Many authors have discussed the utility of competitive learning in the dentate gyrus to orthogonalize the patterns before they are presented to the CA3 network, as suggested by Rolls (1987). Marr (1971) had previously noted the desirability of such a mathematical operation, McNaughton and Morris (1987) referred to detonating synapses in the dentate to CA3 projection, and Treves and Rolls (1992, 1994) produced a formal analysis of the process.

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