Neurophysiology of the primate hippocampus leading to a model of its functions in episodic and spatial memory

Edmund T. Rolls and Simon M. Stringer
Oxford University
Centre for Computational Neuroscience
Department of Experimental Psychology
South Parks Road
Oxford OX1 3UD
England
E-mail: Edmund.Rolls@psy.ox.ac.uk
web: www.cns.ox.ac.uk

Abstract—Recordings from single hippocampal neurons in locomoting macaques reveal that some cells are tuned to "spatial view". Other neurons respond to objects, or a combination of an object and its spatial position, forming the basis for an attractor model of episodic memory combining continuous and discrete representations which is described. Spatial view cells (in conjunction with whole body motion cells in the primate hippocampus, and head direction cells in the primate presubiculum [1]) would be useful as part of a spatial navigation system, for which they would provide a memory component. Given that idiothetic (self-motion) cues such as eye movements update the spatial view representation in the dark, path integration as well as memory is implemented. In a model of this, it is proposed that the hippocampal system incorporates a continuous attractor network for the spatial representation that can be moved in the state space by idiothetic inputs [2], [3].

I. INTRODUCTION

Recordings from single hippocampal neurons in locomoting macaques reveal that some cells are tuned to "spatial view". These hippocampal neurons (1) respond to a view of space "out there", not to the place where the monkey is; (2) have responses that depend on where the monkey is looking, as shown by measuring eye position; (3) can still occur (especially for CA1 neurons) if the view details are obscured with curtains; (4) retain part of their "space" tuning even in complete darkness for several minutes; (5) have an allocentric spatial representation; and (6) convey information about spatial view that increases linearly with the number of cells in the representation [4]. The spatial representation may be different from that of place cells in rats because of the smaller field of view of primates [5]. Spatial view cells (in conjunction with whole body motion cells in the primate hippocampus, and head direction cells in the primate presubiculum [1]) would be useful as part of a spatial navigation system, for which they would provide a memory component. Given that idiothetic (self-motion) cues such as eye movements update the spatial representation in the dark, path integration as well

as memory is implemented. It has also been shown that some hippocampal cells encode for objects, others for places in a room, and others for combination of objects and places, while a monkey is performing an object-place memory task. This task is prototypical of episodic memory, and provides evidence that the primate hippocampus does link associatively information about objects and allocentric information about places out there.

An established approach to modelling neurons which encode spatial information is the *continuous attractor neural network* (CANN). Continuous attractor networks have previously been used for modelling head direction cells [6], [7], [8] and place cells [9], [10], [11]. This class of network can maintain the firing of its neurons to represent any location along a continuous physical dimension such as head direction, spatial location, or spatial view. These models use excitatory recurrent collateral connections between the neurons to reflect the distance between the neurons in the state space (e.g. head direction space) of the animal. Global inhibition is used to keep the number of neurons in a bubble of activity relatively constant, and to ensure there is only one activity packet.

In this paper we show how a single network, such as the hippocampal CA3 network, could combine discrete representations of objects with continuous representations of space to form an episodic memory. Then we show how a continuous attractor model of spatial view cells could be updated by self-motion (idiothetic) inputs. Finally, we show how a single continuous attractor network can support multiple activity packets in separate feature spaces. This permits the network to represent the full 3D spatial structure of the environment, which is important for navigation through cluttered environments.

631

II. MAIN RESULTS

A. Combining discrete and continuous memories in an object-place model of episodic memory

Most models of hippocampal function have focussed primarily on networks that can store discrete patterns suitable for episodic memory [12], [13], [14], [15], [16], or on continuous patterns suitable for spatial memory [10], [9], [17], [3]. However, there is evidence from single unit recording studies that both types of memory pattern must exist in the same networks in the brain. For example, it has been shown that some hippocampal cells encode for objects, others for places in a room, and others for combination of objects and places, while a monkey is performing an object-place memory task [18]. This task is prototypical of episodic memory, and provides evidence that the primate hippocampus does link associatively information about objects and allocentric information about places out-there.

In [19] we analysed an attractor network that could store both continuous (e.g. spatial) patterns and discrete (e.g. single object) patterns, as illustrated in Fig. 1. The model consists of a single attractor network with excitatory modifiable connections between the neurons. This model unifies the spatial and episodic approaches to medial temporal lobe function by showing how both types of representation can be stored in the same network, which is necessary if associations between them are to be learned and retrieved.

A   Memory 1

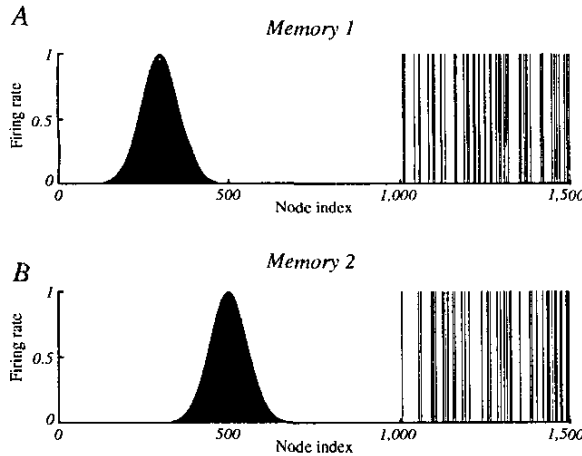B   Memory 2

Fig. 1. The firing patterns for two different memories (1 and 2) of nodes 1-1000 which represent the spatial firing and nodes 1001-1500 which represent the discrete events that occur at the location. The continuous nature of the spatial representation results from the fact that each neuron has a Gaussian firing rate that peaks at its optimal location. Fig. 1A shows the firing rates of the set of active neurons when the animal is located at the location at which neuron 300 fires maximally, while Fig. 1B shows the activity of the spatial and event neurons when the animals is at location 500. During learning, memory 1 is stored in the synaptic weights, then memory 2, etc, and each memory contains part which is continuously distributed to represent physical space, and part which represents a discrete event.

In simulations, the 1500 neurons within the attractor network were divided into two classes of cells with different response properties, of the type illustrated in Fig. 1. Nodes 1–1000 provided a spatial representation, with each neuron tuned to have Gaussian firing as a function of location consistent with place cells in rats and spatial view cells in primates. More precisely, the firing rate of the spatial cells was a Gaussian function of the displacement of the agent from the optimal firing location of the cell in the space. Nodes 1001–1500 represented discrete objects/events. Each 'object' was represented by a set of 50 of these 500 cells in the active (1) state, with the remaining cells in the inactive (0) state, that is the sparseness of the (orthogonal) representations was 0.1. Two examples of the resulting stimulus patterns that were presented during learning to the single attractor network are illustrated in Fig. 1.
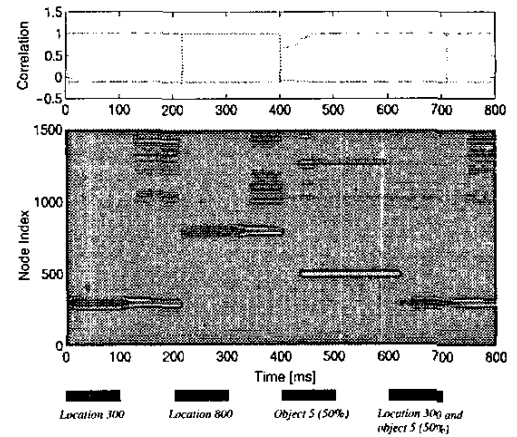

Fig. 2. The performance during and after external stimulation of the trained network. Lower: The firing of each node is shown as a function of time in ms. (The time constant of the dynamics of the neurons was 10 ms.) Nodes 1-1000 reflect the spatial component of the memory, and nodes 1001-1500 represent the discrete event that is a part of each memory. Retrieval cues were applied as shown to location 300 and later to location 800, and in each case the correct discrete object representation was retrieved. Object 5 applied as a retrieval cue retrieved the correct spatial location. The last retrieval cue is an inconsistent object-place combination, and when the cue was removed, one of the trained episodic memories was retrieved. Upper: Retrieval in the event nodes, shown by the correlation between the recalled state of firing and the stored state for each of the trained discrete events represented by the activity of nodes 1001-1500.

Identical training is used for the two types of pattern. The network was trained at 50 equispaced locations, at 10 of which discrete objects were present. At each training location, the recurrent collateral synaptic weights between the nodes are modified with an associative (Hebbian) rule

$$\delta w_{ij} = k r_i r_j, \tag{1}$$

where δw_{ij} is the change in the synaptic weight w_{ij} from node j to node i, r_i is the firing rate of the postsynaptic node i, r_j is the firing rate of the presynaptic node j, and k is the learning rate.

The time evolution of the system was simulated according

632

to the continuous dynamics of leaky integrator neurons

$$\tau\frac{dh_i(t)}{dt} = -h_i(t) + \frac{\phi_0}{C}\sum_j(w_{ij} - w^{INH})r_j(t) + I_i^{EXT} \quad (2)$$

and

$$r_i(t) = \frac{1}{1 + e^{-2\beta(h_i(t)-\alpha)}}, \quad (3)$$

where h_i is the activity of node i, r_i the corresponding firing rate, I_i^{EXT} is the synaptic current produced by an external input, and w_{ij} is an excitatory (positive) synaptic weight from node j to node i trained with rule 1. The parameter w^{INH} governs the level of inhibition between the neurons.

Simulation results are shown in Fig. 2, and details are provided in [19].

B. An attractor network of spatial view cells with idiothetic update

In primates, single neuron recording studies have demonstrated the existence of spatial view cells in the primate hippocampus that respond when the monkey is looking towards a particular location in allocentric space [20], [21], [22], [23], [24]. Spatial view cells update their spatial representations by idiothetic inputs in the dark, in that if the monkey moves his head and eyes to look at the effective spatial location, then the neurons fire [23]. Part of the interest of these primate spatial view neurons is that they represent a place at which a primate is looking, and could therefore be involved in functions such as providing the spatial representation needed for remembering where an object is in space, and in general for representing places at which one is not actually located [20], [19].

In [3] and [25] we developed continuous attractor models of head direction and rat place cells which differed from previous models [6], [7], [9], [10], [11] in that they are able to self-organise during training the synaptic connections used for the idiothetic path integration. We now describe how these models can be extended to primate spatial view cells [26]. The inputs used for the idiothetic update of spatial cells in the primate hippocampus must be very different from those in rats, for in primates the allocentric location is idiothetically updated by eye position as well as by head direction [23], and no eye position update has ever been suggested for the rat. Thus, models of spatial view cells must address how different types of input that reflect eye position and head direction information could be utilized in a path integration continuous attractor neural network. A major challenge is that two idiothetic signals, which separately reflect eye position and head direction, need to be combined in the path integration process, and this had not been treated in previous self-organizing continuous attractor models. We describe here the first of the models developed in [26].

The network architecture is shown in Fig. 3. When visual input is available, each spatial view cell responds with a Gaussian profile to a view of part of the environment, and that part of the environment can be looked at with a given gaze angle which is provided by a combination of head direction and eye position signals. The spatial view cells are connected

by recurrent collateral synapses that reflect the distance in the state space (in this case the spatial view) of any two connected cells. The strengths of these synaptic connections of the continuous attractor network are trained by an associative Hebb rule while the agent explores the environment. The correct synaptic weights are set up because spatial view cells that are close in view space will tend to be coactive. That is, during learning the recurrent weights w_{ij}^{RC} from spatial view cell j with firing rate r_j^{SV} to spatial view cell i with firing rate r_i^{SV} are altered according to

$$\delta w_{ij}^{RC} = k^{RC}r_i^{SV}r_j^{SV} \quad (4)$$

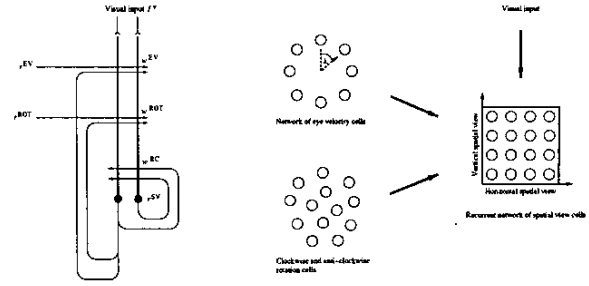where δw_{ij}^{RC} is the change of synaptic weight, and k^{RC} is the learning rate constant.

Fig. 3. General network architecture of CANN model of spatial view cells. There is a recurrent layer of spatial view cells in which the cells are mapped onto a regular grid of spatial views. The spatial views are defined by the angle of gaze of the agent. In the light, individual spatial view cells are stimulated maximally when the agent has an angle of gaze corresponding to the position of the cell in the grid. The layer of spatial view cells receives external inputs from 3 sources: (i) the visual system, (ii) a population of clockwise and anti-clockwise rotation cells, and (iii) a population of eye velocity cells. The clockwise and anti-clockwise rotation cells fire according to whether the agent is rotating in the appropriate direction, and with a firing rate that increases monotonically with respect to the speed of rotation. The eye velocity cells fire maximally when an animal moves its eyes in a particular direction, and have firing rates that increase with the speed of movement of the eyes. The velocity of the animal's eyes is denoted by (v, λ) where v is the angular speed of movement of the eyes, and λ is the direction of movement of the eyes. The eye velocity cells are mapped onto a circular grid of directions of eye movement, where each eye velocity cell has a unique direction of eye movement for which the cell fires maximally.

Now we consider the self-organization of the idiothetic synaptic weights w_{ijk}^{ROT} from the head rotation cells. The essence of this learning process is that when the activity packet in the spatial view cell continuous attractor has moved, say, in a clockwise direction, a trace term in a set of synaptic connections between the spatial view cells "remembers" the direction in which the spatial view cells have been activated, and this term is associated by learning with the current head rotation velocity cell input and the firing of the postsynaptic spatial view cell receiving both inputs. More formally, the synaptic weights w_{ijk}^{ROT} are updated at each timestep during motion through the environment in a self-organizing learning process according to

$$\delta w_{ijk}^{ROT} = k^{ROT}r_i^{SV}\bar{r}_j^{SV}r_k^{ROT} \quad (5)$$

where δw_{ijk}^{ROT} are the changes in the synaptic weights, and where r_i^{SV} is the instantaneous firing rate of the postsynaptic

633

spatial view cell i, $\bar{r}_j^{SV}$ is the trace value of the presynaptic spatial view cell j given by Equation (6), r_k^{ROT} is the firing rate of rotation cell k, and k^{ROT} is the learning rate associated with this type of synaptic connection. In equation (5) $\bar{r}^{SV}$ is a local temporal average or memory trace value of the firing rate of a spatial view cell given by

$$\bar{r}^{SV}(t + \delta t) = (1 - \eta)r^{SV}(t + \delta t) + \eta\bar{r}^{SV}(t) \qquad (6)$$

where η is a parameter set in the interval $[0,1]$ which determines the relative contributions of the current firing and the previous trace.

In a similar way, the idiothetic synaptic weights, w_{ijk}^{EV}, from the eye velocity cells are set up according to

$$\delta w_{ijk}^{EV} = k^{EV} r_i^{SV} \bar{r}_j^{SV} r_k^{EV} \qquad (7)$$

where δw_{ijk}^{EV} is the change of synaptic weight, r_i^{SV} is the instantaneous firing rate of spatial view cell i, $\bar{r}_j^{SV}$ is the trace value of the firing rate of spatial view cell j given by equation (6), r_k^{EV} is the firing rate of eye velocity cell k, and k^{EV} is the learning rate associated with this type of connection.

The activation $h_i^{SV}(t)$ of each spatial view cell i is governed by

$$
\begin{aligned}
\tau\frac{dh_i^{SV}(t)}{dt} &= I_i^V - h_i^{SV}(t) \\
&+ \frac{\phi_0}{C^{SV}} \sum_j (w_{ij}^{RC} - w^{INH})r_j^{SV}(t) \\
&+ \frac{\phi_1}{C^{SV \times ROT}} \sum_{j,k} w_{ijk}^{ROT} r_j^{SV} r_k^{ROT} \\
&+ \frac{\phi_2}{C^{SV \times EV}} \sum_{j,k} w_{ijk}^{EV} r_j^{SV} r_k^{EV}.
\end{aligned}
\qquad (8)
$$

The term r_j^{SV} is the firing rate of spatial view cell j, w_{ij}^{RC} is the excitatory (positive) synaptic weight from spatial view cell j to spatial view cell i, and w^{INH} is a global constant describing the effect of inhibitory interneurons within the layer of spatial view cells. The term I_i^V represents a visual input to spatial view cell i, and τ is the time constant of the system. In the absence of visual input there are two key input terms driving the cell activations in equation (8) as follows. Firstly, there are idiothetic inputs from the rotation cells, $\sum_{j,k} w_{ijk}^{ROT} r_j^{SV} r_k^{ROT}$, where r_k^{ROT} is the firing rate of rotation cell k, and w_{ijk}^{ROT} is the corresponding overall effective strength of connection from this cell. Secondly, there is an idiothetic input from the eye velocity cells $\sum_{j,k} w_{ijk}^{EV} r_j^{SV} r_k^{EV}$ where r_k^{EV} is the firing rate of eye velocity cell k and w_{ijk}^{EV} is the corresponding overall effective strength of connection.

Once the activations of the spatial view cells have been computed, the firing rates of the cells are then given by the sigmoid transfer function

$$r_i^{SV}(t) = \frac{1}{1 + e^{-2\beta(h_i^{SV}(t) - \alpha)}}, \qquad (9)$$

where α and β are the sigmoid threshold and slope, respectively.

Fig. 4 shows performance after training. On the left it is shown that if there are no visual and idiothetic inputs, there is a stable firing rate profile within the continuous attractor network of spatial view cells. It is shown in the right plot that the spatial view activity packet moves in the correct direction (in the absence of visual inputs) when the agent: (i) rotates its head clockwise, (ii) moves its eyes upwards, and (iii) simultaneously rotates its head clockwise and moves its eyes upwards. This important result demonstrates that, after the synaptic weights have been set up through learning, the two different types of idiothetic inputs to the layer of spatial view cells, from the rotation cells and from the eye velocity cells, are able to operate together as the agent rotates and moves its eyes in the dark.
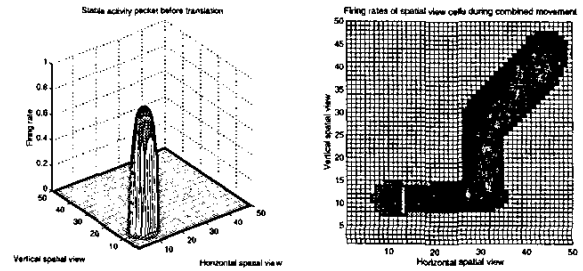

Fig. 4. Simulation results of CANN model of spatial view cells. The plot shows the firing rates within the continuous attractor network of spatial view cells during the testing phase with the agent in the dark. The grid shows the horizontal and vertical coordinates at which the different spatial view cells have their optimal firing. Left: Stable firing rate profile within the network of spatial view cells before the agent starts to move. Right: Maximum firing rates that occurred during movement of the agent in the testing phase. (The maximum firing rate is calculated over all timesteps for each spatial view cell.) Firstly, the agent rotated its head in the clockwise direction. Next the agent moved its eyes vertically upwards. Finally, the agent simultaneously rotated its head in the clockwise direction and moved its eyes vertically upwards.

An interesting situation arises when the agent is free to perform more than one movement at a time during learning. For example, consider the case where the agent may rotate its head clockwise and move its eyes vertically upwards at the same time. In this case the network will associate the overall movement of the agent's spatial view, which will be a diagonal path in a direction of 45° as shown in the right plot of Fig. 4, independently with each of the two separate idiothetic velocity signals, clockwise head rotation and vertical eye movement. Stringer et al. have investigated this issue in [26], where a further model is developed which associates specific combinations of movement signals with the shift of the activity packet in the continuous attractor network of spatial view cells.

C. CANNs with multiple activity packets, and the 3D representation of space

In the applications of continuous attractor networks discussed above, where a network is required to represent only a single state of the agent (i.e. head direction, place or spatial view), it is appropriate for the continuous attractor networks to support only one activity packet at a time. In [27] we proposed

634

that continuous attractor networks may be used in the brain in an alternative way, in which they support multiple activity packets at the same time. To elaborate, each neuron in the network might represent a particular class of feature (such as a straight edge, or red color) in a particular egocentric location in the environment. Thus, each class of feature is represented by a different set of neurons, where each of the neurons responds to the presence of a feature at a particular location. The different sets of neurons that encode the different features may have many cells in common and so significantly overlap with each other, or may not have cells in common in which case each neuron will respond to no more than one feature. For each type of feature, the ordering in the network of the neurons that represent the location of the feature in space is random. Therefore, each separate feature space has a unique ordering of neurons which we refer to as a 'map'. However, all the feature maps are encoded in the same network. The presence of a particular feature at a particular location in the environment is represented by an activity packet centred at the appropriate location in the map which is associated with that particular feature. Since the network is able to maintain and update the representations of many different (e.g. shape) features simultaneously (which implies binding) using an idiothetic signal, this means that the network is able to maintain a full 3-dimensional representation of the spatial structure of an agent's environment, even as the agent moves within its environment in the absence of visual input.

Fig. 5 shows simulation results with two activity packets active in two different feature spaces, x^μ and x^ν, in the same continuous attractor network of feature cells. The spaces x^μ and x^ν are closed 1D toroidal spaces, which represent the egocentric locations (bearing) of two different kinds of spatial feature μ and ν in an agent's environment. In this experiment the network is trained with two features, μ and ν. During training, the agent rotates clockwise on the spot, which causes the two features to move through their corresponding egocentric location spaces. At the same time, idiothetic cells which represent the clockwise rotation of the agent become active. The synaptic connection strengths from idiothetic cells to the feature cells within the continuous attractor network are then self-organised using the trace learning rule

$$\delta w_{ijk}^{\text{ID}} = k^{\text{ID}} r_i^{\text{F}} \bar{r}_j^{\text{F}} r_k^{\text{ID}} \qquad (10)$$

where $\delta w_{ijk}^{\text{ID}}$ is the change of synaptic weight, r_i^{F} is the instantaneous firing rate of feature cell i, $\bar{r}_j^{\text{F}}$ is the trace value (temporal average) of the firing rate of feature cell j, r_k^{ID} is the firing rate of idiothetic cell k, and k^{ID} is the learning rate. The recurrent connections between the feature cells in the continuous attractor network are self-organised during learning using an associative (Hebb) learning rule similar to that described above for the spatial view cells.

The continuous attractor network is composed of 5000 feature cells. In the simulations presented here, 1000 of these cells are stimulated during the learning phase by visual input from feature μ. This subset of 1000 feature cells is denoted Ω^μ, and it is this subset of cells that is used to encode the

location space for feature μ. Similarly, a further 1000 feature cells are stimulated during the learning phase by visual input from feature ν. This subset of 1000 feature cells is denoted Ω^ν, and it is this subset of cells that encodes the location space for feature ν. For this experiment the two subsets, Ω^μ and Ω^ν, are chosen randomly from the total network of 5000 feature cells, and so the subsets significantly overlap. During the learning phase, the subset Ω^μ of feature cells is evenly distributed along the 1-dimensional space x^μ (and correspondingly for the Ω^ν cells in the x^ν space). The training is performed separately with 10 revolutions for each of the two spaces. From these results we see that the continuous attractor network of feature cells is able to maintain activity packets active in the two different feature spaces x^μ and x^ν. Furthermore, as the agent moves, the network representations of the egocentric locations of the features may be updated by idiothetic signals. Theoretical analyses and computer simulations presented in [27] showed that as the number of neurons in the network increased, the interference between activity packets in separate spaces diminished. This important result supports the hypothesis that large recurrent networks in the brain are able to maintain multiple activity packets, perhaps representing different features in different locations in the environment.
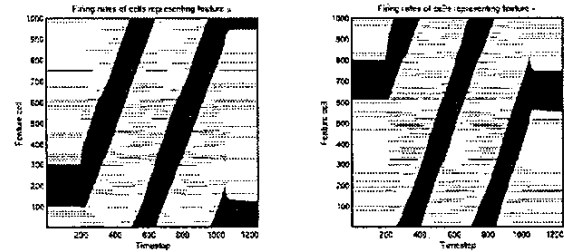

Fig. 5. Simulation of CANN with two activity packets active in two different feature spaces, x^μ and x^ν, in the same continuous attractor network of feature cells. In this experiment the two feature spaces significantly overlap, i.e. they have feature cells in common. Nevertheless, path integration in each of the spaces is demonstrated. The network thus represents the presence of two different types of feature, μ and ν, in the environment. The left plot shows the firing rates of the subset of feature cells Ω^μ belonging to the first feature space x^μ, and the right plot shows the firing rates of the subset of feature cells Ω^ν belonging to the second feature space x^ν. Furthermore, in the plot on the left the feature cells have been ordered according to the order they occur in the first feature space, and in the plot on the right the feature cells have been ordered according to the order they occur in the second feature space. Thus, the left and right plots show the two activity packets moving within their respective feature spaces.

A key problem with current models of hippocampal place cells [28] is the inability of the representations supported by these neural networks to provide a basis for planning novel routes through complex environments full of obstacles. Current models of place cells assume a single activity packet in a 2-dimensional layer of place cells, where the cells are simply mapped onto the floor of the containment area. However, such a representation merely locates the agent in a 2-dimensional space, and cannot provide information about the full 3-dimensional structure of the surrounding environment, which

635

would be necessary for planning a novel route along paths and past obstacles, etc. However, the multi-packet continuous attractor models described in [27] offer a solution to how the full 3-dimensional structure of the surrounding environment might be represented, and how this representation may be updated through idiothetic signals or motor efference copy. Only such a representation of the full 3-dimensional structure of the agent's environment will provide a robust basis for planning novel routes in complex, cluttered environments.

III. CONCLUSIONS

In this paper we demonstrated how continuous spatial representations can be combined with discrete object representations within a single continuous attractor neural network. This is prototypical for an episodic memory. We then went on to show how path integration might be performed in a network of spatial view cells using head rotation and eye velocity signals. Lastly we showed how multiple representations may be kept active within a single attractor network, and how the separate activity packets may be simultaneously updated using idiothetic velocity signals. Although not shown in this paper, the present findings provide a framework for understanding how the idiothetic connections within a multiple-space/multiple-packet CANN are able to self-organise such that, after training, the activity packets in the different spaces may be updated by different kinds of idiothetic velocity signals. This would permit a population of head direction cells and a population of spatial view cells to co-exist within the same attractor network, and to be independently updated by different kinds of idiothetic signals which are appropriate to each space. There are a number of different kinds of velocity signals that might be used to update spatial representations in the brain during movement in the absence of visual cues. In [29] we showed how the spatial representations within a CANN may be updated by motor efference copy in a combined network of state and motor cells. An important issue for future research is how path integration networks in the brain, which may represent spatial information in multiple spaces or frames of reference, are able to learn to combine multiple velocity signals of different kinds such as head rotation, eye velocity, and motor efference copy signals.

ACKNOWLEDGMENT

REFERENCES

[1] R. G. Robertson, E. T. Rolls, P. Georges-François, and S. Panzeri, "Head direction cells in the primate pre-subiculum," *Hippocampus*, vol. 9, pp. 206–219, 1999.

[2] E. T. Rolls and G. Deco, *Computational Neuroscience of Vision*. Oxford: Oxford University Press, 2002.

[3] S. M. Stringer, T. P. Trappenberg, E. T. Rolls, and I. E. T. de Araujo, "Self-organizing continuous attractor networks and path integration: One-dimensional models of head direction cells," *Network: Computation in Neural Systems*, vol. 13, pp. 217–242, 2002.

[4] E. T. Rolls, "Spatial view cells and the representation of place in the primate hippocampus," *Hippocampus*, vol. 9, pp. 467–480, 1999.

[5] I. E. T. de Araujo, E. T. Rolls, and S. M. Stringer, "A view model which accounts for the response properties of hippocampal primate spatial view cells and rat place cells," *Hippocampus*, vol. 11, pp. 699–706, 2001.

[6] A. D. Redish, A. N. Elga, and D. S. Touretzky, "A coupled attractor model of the rodent head direction system," *Network: Computation in Neural Systems*, vol. 7, pp. 671–685, 1996.

[7] K. Zhang, "Representation of spatial orientation by the intrinsic dynamics of the head-direction cell ensemble: A theory," *Journal of Neuroscience*, vol. 16, pp. 2112–2126, 1996.

[8] P. E. Sharp, H. T. Blair, and J. Cho, "The anatomical and computational basis of the rat head-direction cell signal," *Trends in Neurosciences*, vol. 24, pp. 289–294, 2001.

[9] A. D. Redish and D. S. Touretzky, "The role of the hippocampus in solving the Morris water maze," *Neural Computation*, vol. 10, pp. 73–111, 1998.

[10] A. Samsonovich and B. McNaughton, "Path integration and cognitive mapping in a continuous attractor neural network model," *Journal of Neuroscience*, vol. 17, pp. 5900–5920, 1997.

[11] M. Tsodyks, "Attractor neural network models of spatial maps in hippocampus," *Hippocampus*, vol. 9, pp. 481–489, 1999.

[12] D. Marr, "Simple memory: a theory for archicortex," *Philosophical Transactions of the Royal Society, London [B]*, vol. 262, pp. 23–81, 1971.

[13] A. Treves and E. T. Rolls, "Computational constraints suggest the need for two distinct input systems to the hippocampal CA3 network," *Hippocampus*, vol. 2, pp. 189–199, 1992.

[14] ——, "A computational analysis of the role of the hippocampus in memory," *Hippocampus*, vol. 4, pp. 374–391, 1994.

[15] J. L. McClelland, B. L. McNaughton, and R. C. O'Reilly, "Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory," *Psychological Review*, vol. 102, pp. 419–457, 1995.

[16] E. T. Rolls, "A theory of hippocampal function in memory," *Hippocampus*, vol. 6, pp. 601–620, 1996.

[17] M. Tsodyks, "Attractor neural network models of spatial maps in hippocampus," *Hippocampus*, vol. 9, pp. 481–489, 1999.

[18] E. T. Rolls, J.-Z. Xiang, and L. Franco, "Object, space and object-space representations in the primate hippocampus," *in prep*, 2004.

[19] E. T. Rolls, S. M. Stringer, and T. P. Trappenberg, "A unified model of spatial and episodic memory," *Proceedings of The Royal Society B*, vol. 269, pp. 1087–1093, 2002.

[20] E. T. Rolls, "Spatial view cells and the representation of place in the primate hippocampus," *Hippocampus*, vol. 9, pp. 467–80, 1999.

[21] E. T. Rolls, R. G. Robertson, and P. Georges-François, "Spatial view cells in the primate hippocampus," *European Journal of Neuroscience*, vol. 9, pp. 1789–1794, 1997.

[22] P. Georges-François, E. T. Rolls, and R. G. Robertson, "Spatial view cells in the primate hippocampus: allocentric view not head direction or eye position or place," *Cerebral Cortex*, vol. 9, pp. 197–212, 1999.

[23] R. G. Robertson, E. T. Rolls, and P. Georges-Francois, "Spatial view cells in the primate hippocampus: effects of removal of view details," *Journal of Neurophysiology*, vol. 79, pp. 1145–1156, 1998.

[24] E. T. Rolls, A. Treves, R. G. Robertson, P. Georges-Francois, and S. Panzeri, "Information about spatial view in an ensemble of primate hippocampal cells," *Journal of Neurophysiology*, vol. 79, pp. 1797–1813, 1998.

[25] S. M. Stringer, E. T. Rolls, T. P. Trappenberg, and I. E. T. de Araujo, "Self-organizing continuous attractor networks and path integration: Two-dimensional models of place cells," *Network: Computation in Neural Systems*, vol. 13, pp. 429–446, 2002.

[26] S. M. Stringer, E. T. Rolls, and T. P. Trappenberg, "Self-organizing continuous attractor network models of hippocampal spatial view cells," *in prep*, 2004.

[27] ——, "Self-organising continuous attractor networks with multiple activity packets, and the representation of space," *Neural Networks*, vol. 17, pp. 5–27, 2004.

[28] A. D. Redish, *Beyond the Cognitive Map: From Place Cells to Episodic Memory*. Cambridge, Massachusetts: MIT Press, 1999.

[29] S. M. Stringer, E. T. Rolls, T. P. Trappenberg, and I. E. T. de Araujo, "Self-organizing continuous attractor networks and motor function," *Neural Networks*, vol. 16, pp. 161–182, 2003.