

Modelling spatial recall, mental imagery and neglect

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Abstract

We present a computational model of the neural mechanisms in the parietal and temporal lobes that support spatial navigation, imagery, and episodic recall. Long term representations are stored in the hippocampus, and are associated with local spatial and object-related features in the parahippocampal region. Viewer-centered representations are dynamically generated from long term memory in the parietal part of the model. The model thereby simulates recall and imagery of locations and objects in complex environments. After parietal damage, the model exhibits hemispatial neglect in mental imagery that rotates with the imagined perspective of the observer, as in the famous Milan Square experiment reported by Bisiach and Luzatti [1]. Our model makes novel predictions for the neural representations in the parahippocampal and parietal regions and for behavior in healthy volunteers and neuropsychological patients.

1 Introduction

We perform spatial computations everyday. Tasks such as reaching and navigating around visible obstacles are predominantly sensory-driven rather than memory-based, and presumably rely upon *egocentric*, or viewer-centered representations of space. These representations, and the ability to translate between them, have been associated with the parietal cortex, and several computational models of this region have been proposed, e.g. [2, 3]. In other situations such as route planning and scene recall, one must also rely upon representations of spatial layouts from long-term memory. Neuropsychological and neuroimaging studies implicate both the parietal and hippocampal regions in such tasks [4], with the long-term memory component

associated with the hippocampus. The discovery of “place cells” in the hippocampus [5] provides evidence that hippocampal representations are *allocentric*, in that absolute locations in open spaces are encoded irrespective of viewing direction.

This paper addresses the nature and source of the spatial representations in the hippocampal and parietal regions, and how they interact with each other during recall and navigation. We assume that in the hippocampus proper, long-term spatial memories are stored allocentrically, whereas in the parietal cortex view-based images are created on-the-fly during perception or recall. Intuitively it makes sense to use an allocentric representation for long-term storage as the position of the body will have changed before recall. Alternatively, to act on a spatial location (e.g. reach with the hand) or to imagine a scene an egocentric representation (e.g. relative to the hand or retina) is more useful.

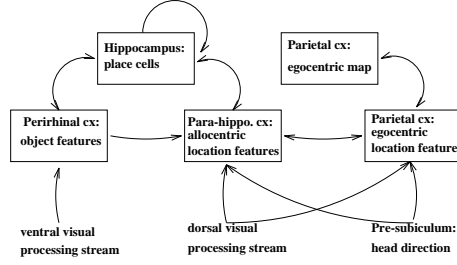
A study of hemispatial neglect patients throws some light on the interaction of long-term memory with mental imagery. Bisiach and Luzatti [1] asked two patients to recall the buildings from the familiar Cathedral Square in Milan, (i) after being asked to imagine facing the cathedral, and (ii) after being asked to imagine facing in the opposite direction. Both patients, in both (i) and (ii), predominantly recalled buildings that would have appeared on their right from the specified viewpoint. Since the buildings recalled in (i) were located physically on the opposite side of the square to those recalled in (ii), the patients’ long-term memory for all of the buildings in the square was apparently intact. Further, the area neglected rotated according to the patient’s imagined viewpoint, suggesting that their impairment relates to the generation of egocentric mental images from a non-egocentric long-term store.

The model also addresses how information about object identity is bound to locations in space in long-term memory, i.e. how the “what” and the “where” pathways interact. As shown in Figure 1a, object information from the ventral visual processing stream enters the hippocampal formation (medial entorhinal cortex) via the perirhinal cortex, while visuospatial information from the dorsal pathways enters lateral entorhinal cortex primarily via the parahippocampal cortex [6]. We extend the O’Keefe & Burgess [7] hippocampal model to include object-place associations by encoding object features in perirhinal cortex (we refer to these features as texture, but they could also be attributes such as colour, shape or size). Reciprocal connections to the parahippocampus allow object features to cue the hippocampus to activate a remembered location in an environment, and conversely, a remembered location can be used to reactivate the feature information of objects at that location. The connections from parietal to parahippocampal areas allow the remembered location to be specified in egocentric imagery.

2 The model

The model may be thought of in simple terms as follows. An allocentric representation of object location is extracted from the ventral visual stream in the parahippocampus, and feeds into the hippocampus. The dorsal visual stream provides an egocentric representation of object location in medial parietal areas and makes bi-directional contact with the parahippocampus via posterior parietal area 7a. Inputs carrying allocentric heading direction information [8] project to both parietal and parahippocampal regions, allowing bidirectional translation from allocentric to

a)



b)

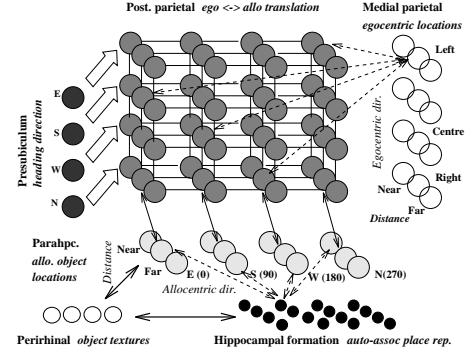


Figure 1: The model architecture.

egocentric directions. Recurrent connections in the hippocampus allow recall from long-term memory via the parahippocampus, and egocentric imagery in the medial parietal areas. We describe the model in more detail below.

2.1 Hippocampal system

The architecture of the model is shown in Figure 1b. The hippocampal formation (HF) consists of several regions – the entorhinal cortex, dentate gyrus, CA3, and CA1, each of which appears to code for space with varying degrees of sparseness. To simplify, in our model the HF is represented by a single layer of “place cells”, each tuned to random, fixed configurations of spatial features as in [7]. Additionally, it learns to represent objects’ textural features associated with a particular location in the environment. It receives these inputs from the parahippocampal cortex (PH) and perirhinal cortex (PR), respectively.

The parahippocampal representation of object locations is simulated as a layer of neurons, each of which is tuned to respond whenever there is a landmark at a given distance and allocentric direction from the subject. Projections from this representation into the hippocampus drive the firing of place cells. This representation has been shown to account for the properties of place cells recorded across environments of varying shape and size [7]. Recurrent connections between place cells allow for subsequent pattern completion in the place cell layer. Return projections to the parahippocampus allow reactivation of all landmark location information consistent with the subject’s current location indicated by the place cells.

The perirhinal representation in our model consists of a layer of neurons, each tuned to a particular textural feature. This region is reciprocally connected with the hippocampal formation [9]. Thus, in our model, object features can be used to cue the hippocampal system to activate a remembered location in an environment, and conversely, a remembered location can activate all associated object textures. Further, each allocentric spatial feature unit in the parahippocampus projects to the perirhinal object feature units so that attention to one location can activate a particular object’s features.

2.2 Parietal cortex

Neurons responding to specific egocentric stimulus locations (e.g. relative to the eye, head or hand) have been recorded in several parietal areas. Tasks involving imagery tend to activate medial parietal areas (precuneus, posterior cingulate, retrosplenial cortex) in neuroimaging studies [10]. We hypothesize that there is a medial parietal egocentric map of space, coding for the locations of objects organised by distance and angle from the body midline. In this representation cells are tuned to respond to the presence of an object at a specific distance in a specific egocentric direction. Cells have also been reported in posterior parietal areas with egocentrically tuned responses that are modulated by variables such as eye position [11] or body orientation (in area 7a [12]). Such coding can allow translation of locations between reference frames [13, 2]. We hypothesize that area 7a performs the translation between allocentric and egocentric representations so that, as well as being driven directly by perception, the medial parietal egocentric map can be driven by recalled allocentric parahippocampal representations. This translation requires a modulatory input from the head direction system.

The translation between parahippocampal and parietal representations occurs via a hard-wired mapping of each to an expanded set of egocentric representations, each modulated by head direction so that one is fully activated for each (coarse coded) head direction (see Figure 1b). With activation from the appropriate head direction unit, activation from the parahippocampal or parietal representation can activate the appropriate cell in the other representation via this expanded representation.

2.3 Simulation details

The hippocampal component of the model was trained on the spatial environment shown in the top-left panel of Figure 2, representing the buildings of the Milan square. We generated a series of views of the square, as would be seen from the locations in the central filled rectangular region of this figure panel. The weights were determined as follows. From each training location, each visible edge point contributed the following to the activation of each parahippocampal (PH) cell:

$$A_i^{PH} = \sum_j \sqrt{2\pi\sigma_{ang}^2}^{-1} e^{-\frac{(\theta_i - \theta_j)^2}{2\sigma_{ang}^2}} \times \sqrt{2\pi\sigma_{dir}(r_j)^2}^{-1} e^{-\frac{(r_i - r_j)^2}{2\sigma_{dir}(r_j)^2}} \quad (1)$$

where θ_i and r_i are the preferred object direction and distance of the i th PH cell, θ_j and r_j represent the location of the j th edge point relative to the observer, and σ_{ang} and $\sigma_{dir}(r)$ are the corresponding standard deviations (as in [7]). Here, we used $\sigma_{ang} = \pi/48$ and $\sigma_{dir}(r) = 2(r/10)^2$. The HF place cells were preassigned to cover a grid of locations in the environment, with each cell's activation falling off as a Gaussian of the distance to its preferred location. The PH-HF and HF-PH connection strengths were set equal to the correlations between activations in the parahippocampal and hippocampal regions across all training locations, and similarly, the HF-HF weights were set to values proportional to a Gaussian of the distance between their preferred locations to form a continuous attractor (e.g. [14, 15]).

The weights to the perirhinal (PR) object feature units – on the HF-to-PR and PH-to-PR connections – were trained by simulating sequential attention to one

visible object at a time, from each training location. Thus, a single object's textural features in the PR layer were associated with the corresponding PH location features and HF place cell activations via Hebbian learning. The PR-to-HF weights were trained to associate each training location with the single predominant texture – either that of the nearest object within 5 units distance or that of the background.

The connections to and within the parietal component of the model were hard-wired to implement the bidirectional allocentric-egocentric mappings (these are functionally equivalent to a rotation by adding or subtracting the heading angle). The 2-layer parietal circuit in Figure 1b, essentially encodes separate transformation matrices for each of a discrete set of head directions in the first layer. A right parietal lesion causing left neglect was simulated with graded, random knockout to units in the egocentric map of the left side of space.

After pretraining the model, we performed two sets of simulations. In simulation 1, the model was required to recall the hippocampal representation of the Milan square after being cued with the texture and direction (θ_j) of each of the visible buildings in turn, at a short distance r_j . The PR cells were clamped to the appropriate texture cue, and the PH cells' states, $A^{PH}(t=0)$ were initialized according to equation 1, with $r_j = 2$. The HF place cells and PH spatial feature cells were then repeatedly updated until convergence according to:

$$I^{HF}(t) = .25I^{HF}(t-1) + .75W^{HF-HF} (W^{PH-HF}(2A^{PH}(0) + A^{PH}(t-1)) + W^{PR-HF}A^{PR}) \quad (2)$$

$$A_i^{HF}(t) = \exp(I_i^{HF}(t)) / \sum_k \exp(I_k^{HF}(t)) \quad (3)$$

$$I^{PH}(t) = .9I^{PH}(t-1) + .1W^{HF-PH}A^{HF}(t) \quad (4)$$

$$A_i^{PH}(t) = I_i^{PH}(t) / \sum_k I_k^{PH}(t) \quad (5)$$

In simulation 2 the model was then required generate view-based mental images of the Milan square from various viewpoints according to a specified heading direction. The image was investigated by cueing the model to attend to various locations on the egocentric map, and requiring the model to retrieve the object texture at that location via activation of the PR region. The PH cells and HF place cells were initialized to the states of the retrieved spatial location (obtained after settling in simulation 1). The egocentric medial parietal (MP) activation was then calculated from the PH-to-MP mapping, as described above. Attention to a queried location was simulated by modulating the pattern of activation across the MP layer with a Gaussian filter centered on that location. This activation was then mapped back to the PH layer, and in turn projected to the PR layer via the PH-to-PR connections:

$$I^{PR} = W^{HC-PR}A^{HR} + W^{PH-PR}A^{PH} \quad (6)$$

$$A_i^{PR} = \exp(I_i^{PR}) / \sum_k \exp(I_k^{PR}) \quad (7)$$

2.4 Results and discussion

In simulation 1, when cued with the textures of each of the 5 buildings around the training region, the model settled on an appropriate place cell activation. One such

example is shown in figure 2, upper row, middle panel. The model was cued with the texture of the cathedral front (building 1) and settled to a place representation near to its southwest corner. The resulting PH layer activations are shown in the upper right panel of figure 2 showing correct recall of the locations of the other landmarks around the square. In simulation 2, the model rotated the PH map according to the cued heading direction, and was able to retrieve correctly the texture of each building when queried with its egocentric location. In the lesioned model, buildings to the egocentric left were usually not identified correctly. One such example is shown in the lower four panels of Figure 2. The heading direction is to the south, so building 6 is represented at the top (egocentric forward) of the map. The building to the left has texture 5, and the building to the right has texture 7.

3 Predictions and future directions

We have demonstrated how egocentric spatial representations may be formed from allocentric ones and vice versa. How might these representations and the mapping between them be learned? The entorhinal cortex (EC) is the major cortical input zone to the hippocampus, and both the parahippocampal and perirhinal regions project to it [9]. Single cell recordings in EC indicate tuning curves that are broadly similar to those of place cells, but are much more coarsely tuned and less specific to individual episodes [16, 6]. Additionally, EC cells can hold state information, such as a spatial location or object identity, over long time delays and even across intervening items [6]. An allocentric representation could emerge if the EC is under pressure to use a more compressed, temporally stable code to reconstruct the rapidly changing visuospatial input. An egocentric map is altered dramatically after changes in viewpoint, whereas an allocentric map is not. Thus, the PH and hippocampal representations could evolve via an unsupervised learning procedure that discovers a temporally stable, generative model of the parietal input. The inverse mapping from allocentric PH features to egocentric parietal features could be learned by training the back-projections similarly. But how could the egocentric map in the parietal region be learned in the first place? In a manner analogous to that suggested by Abbott [17], a “hidden layer” trained by Hebbian learning could develop egocentric features in learning a mapping from a sensory layer representing retinally located targets and arbitrary heading directions to a motor layer representing randomly explored (whole-body) movement directions.

So far our simulations have involved a single spatial environment. Place cells recorded from the same rat placed in two similar novel environments show highly similar firing fields [7, 18], whereas after further exposure, distinctive responses emerge (e.g., [19, 20, 18] and unpublished data). In our model, sparse random connections from the object layer to the place layer ensure a high degree of initial place-tuning that should generalize across similar environments. Plasticity in the HF-PR connections will allow unique textures of walls, buildings etc to be associated with particular places; thus after extensive exposure, environment-specific place firing patterns should emerge.

A selective lesion to the parahippocampus should abolish the ability to encode object-place associations altogether, thereby severely disrupting both landmark-based and memory-based navigation. In contrast, a pure hippocampal lesion would spare the ability to represent a single object’s distance and allocentric directions

from a location, so navigation based on a single landmark should be spared. If an arrangement of objects is viewed in a 3-D environment, the recall or recognition of the arrangement from a new viewpoint will be facilitated by having formed an allocentric representation of their locations. Thus we would predict that damage to the hippocampus would impair performance on this aspect of the task, while memory for the individual objects would be unimpaired. Similarly, we would expect a viewpoint-dependent effect in hemispatial neglect patients.

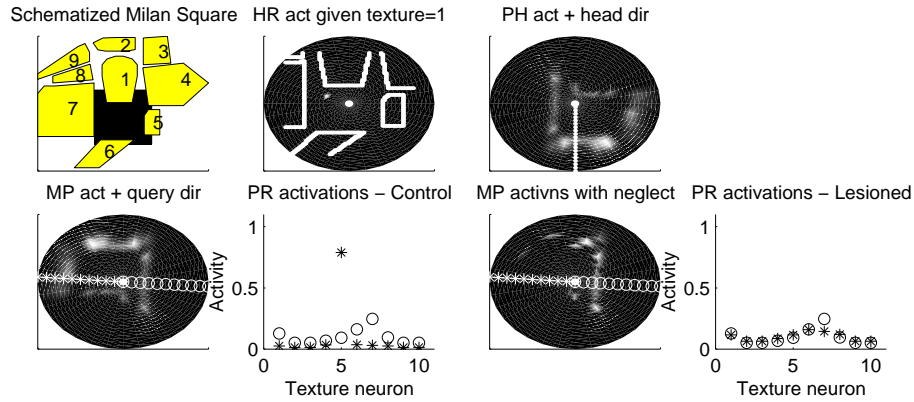


Figure 2: Top: hippocampal and para-hippocampal recall. Bottom: Imagined view (MP), and recalled texture (PR) with attention to right (circles) and left (stars).

One of the many curiosities of the hemispatial neglect syndrome is the temporary amelioration of spatial neglect after placement of cold water into the left ear. Patients commonly report a sensation of head rotation when this happens, although attendant attentional effects may also be relevant. The model predicts that this effect will also be observed in imagery. If the caloric stimulus is evoking erroneous vestibular inputs to shift the perceived head direction system leftward, then all objects will now be mapped further rightward in egocentric space and into the 'good side' of the parietal map in a lesioned model, as is consistent with a recent result [21].

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