Figures and figure supplements

A neural-level model of spatial memory and imagery

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Figure 1. Simplified model schematic. (A) Processed sensory inputs reach parietal areas and support an egocentric representation of the local environment (in a head-centered frame of reference). Retrosplenial cortex uses current head or gaze direction to perform the transformation from egocentric to allocentric coding. At a given location, environmental layout is represented as an allocentric code by activity in a set of BVCs, the place cells (PCs) corresponding to the location, and perirhinal neurons representing boundary identities (in a familiar environment, all these representations are associated via Hebbian learning to form an attractor network). Black arrows indicate the flow of information during perception and memory encoding (bottom-up). Dotted arrows indicate the reverse flow of information, reconstructing the parietal representation from viewpoint invariant memory (imagery, top-down). (B) Illustration of the egocentric (left panel) and allocentric frame of reference (right panel), where the vector $s$ indicates South (an arbitrary reference direction) and the angle $a$ is coded for by head direction cells, which modulate the transformation circuit. This allows BVCs and PCs to code for location within a given environmental layout irrespective of the agent’s head direction (HD). The place field (PF, black circle) of an example PC is shown together with possible BVC inputs driving the PC (broad grey arrows).

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**Figure 2.** Receptive field topology and visualization of neural activity. 

(A1) Illustration of the distribution of receptive field centers (RFs) of place cells (PCs), which tile the environment. (A2) Receptive fields of boundary responsive neurons, be they allocentric (BVCs) or egocentric (PWb neurons), are distributed on a polar grid, with individual receptive fields centered on each delineated polygon. Two example receptive fields (calculated according to **Equation 14**) are overlaid (bright colors) on the polar grids for illustration. Note that each receptive field covers multiple polygons, that is neighboring receptive fields overlap. The polar grids of receptive fields tile space around the agent (red arrow head at center of plots), that is they are anchored to the agent and move with it (for both BVCs and PWb neurons). In addition, for PWb neurons the polar grid of receptive fields also rotates with the agent (i.e. their tuning is egocentric). (B1) As the agent (black arrowhead) moves through an environment, place cells (B2) track its location. (B1) Snapshot of the population activity of all place cells arranged according to the topology of their firing fields (see A1). (C1,2) Snapshots of the population activity for BVCs and boundary selective PW neurons (PWb), respectively. Cells are again distributed according to the topology of their receptive fields (see A2), that is each cell is placed at the location occupied by the centre of its receptive field in peri-personal space (ahead is shown as up for PW neurons; North is shown as up for BVCs). See Section on the transformation circuit, Video 1, and Figure 2—figure supplement 1 for the mapping between PW and BVCs patterns via the transformation circuit. (D1,2) Unlike snapshots of population activity, firing rate maps show the activity of individual neurons averaged over a whole trial in which the agent explores the environment, here for a place cell (D1) and for a boundary vector cell with a receptive field due East (D2, tuning distance roughly 85 cm).

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Figure 2—figure supplement 1. Caption: Illustration of single cell coding in the retrosplenial transformation circuit. Shaded areas indicate the Parietal Window (PWb), the transformation circuit, head direction modulation, and boundary vector cells (BVCs). Example cells are represented as stylized firing rate maps in a simple square environment. Firing related to the North, East, South and West walls is depicted in four colors (blue, yellow, purple, red, respectively). Only 4 PWb cells, 16 transformation circuit neurons, 4 BVCs and four head-direction modulations (North, East, South, West) are shown for simplicity. PWb neurons have egocentric receptive fields (RFs, dashed ovals, shown left of and within each square) that are attached to the agent (black triangle). The RFs respond to boundaries at a specific distance and egocentric direction (ahead, left, right, behind). As the agent moves around the environment, any boundary can fall into the egocentric RF, depending on the agent’s orientation (four example positions and orientations shown), resulting in a firing rate map with firing related to all four boundaries (i.e. the blue, yellow, purple, and red bands, each conditional on the agent facing in a different direction). Considering the PWb cell with the RF ahead of the agent (top left, green star): due to the HD modulation a different RSC cell is receptive to input from that PWb neuron depending on the agent’s current orientation. For example when the agent is facing East the 2nd row of the RSC transformation circuit is receptive to inputs from the PWb, and the first PWb neuron projects to the second cell in that row (green arrow). That RSC cell in turn projects to a BVC with a RF to the East (downward light grey arrow). The Eastward BVC also gets inputs from the other 3 PWb cells when the agent is facing East. The RSC neuron in the 3rd row of the RSC circuit and the BVC in the 2nd row of the boundary vector cells are also receptive to inputs from PWb neurons whose RFs are ahead, right, and left, but not those whose RFs are behind. This circuit allows the agent to constantly update its egocentric position relative to the environment while the HD neuron sends the agent’s current heading (North, East, South, West) to the RSC neurons, which then project to the BVCs to determine the agent’s allocentric position.
Figure 2—figure supplement 1 continued

agent faces in the other three directions, via the other RSC neurons in the second column (connectivity not shown, but indicated by matching symbols: hexagon, triangle, square). Thus, this BVC can fire whenever the agent is near to the East wall, irrespective of the agent’s orientation. In top-down mode (imagery), PWb cells are driven by different BVCs depending on the facing direction of the animal. The PWb cell with the RF ahead of the agent (top left, green star) receives connections from all transformation circuit neurons shown with star symbols: conveying input from the Eastward BVC when facing East, the Northward BVC when facing North etc. In this way, it is driven to fire whenever there is a boundary ahead of the agent. All connections between PWb and BVC cells and transformation circuit neurons are bidirectional, to enable both bottom-up and top-down operation.

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Figure 3. The agent model and population snapshots for object representations. (A) Top panel: The egocentric field of view of the agent (black arrow head). Purple boundaries fall into the forward-facing 180 degree field of view and provide bottom-up drive to the parietal window (PWb; not shown, but see Figure 2C2). The environment contains two discrete objects (green circles). Bottom panel: Allocentric positions of the agent (black triangle) and objects (green circles). (B) Object-related parietal window (PWo) activity (top panel) and OVC activity (bottom panel) due to object 2, South-East of the agent, at time T1. (C) PWo activity (top panel) and OVC activity (bottom panel) due to object 1, North-East of the agent, at time T2. A heuristically implemented attention model ensures that only one object at a time drives the parietal window (PWo). (D) Illustration of the encoding of an object encountered in a familiar environment. Dashed connections are learned (as Hebbian weight updates) between active cells. Solid lines indicate connections learned in the training phase, representing the spatial context. Note that place cells (PCs) anchor the object representation to the spatial context.

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Figure 4. The BB-model. ‘Bottom-up’ mode of operation: Egocentric representations of extended boundaries (PWb) and discrete objects (PWo) are instantiated in the parietal window (PWb/o) based on inputs from the agent model while it explores a simple 2D environment. Attention sequentially modulates object-related PW activity to allow for unambiguous neural representations of an object at a given location. The angular velocity of the agent drives the translation of an activity packet in the head direction ring attractor network. Retrosplenial cortex (RSC) carries out the transformation from egocentric representations in the PW to allocentric representations in the MTL (driving BVCs and OVCs). The transformation circuit consists of 20 sublayers, each maximally modulated by a specific head direction while the remaining circuit is inhibited (Inh). In the medial temporal lobe network, perirhinal neurons (PRb/o) code for the identity of an object or extended boundary. PCs, BVCs and perirhinal neurons are reciprocally connected in an attractor network. Following encoding after object encounters, PCs are also reciprocally connected to OVCs and PRo neurons. ‘Top-down’ mode of operation: Activity in a subset of PCs, BVCs, and/or perirhinal neurons spreads to the rest of the MTL network (pattern completion) by virtue of intrinsic connectivity. With perceptual inputs to the PW disengaged (i.e. during recollection), the transformation circuit reconstructs parietal window (PWb/o) activity based on the current BVC and OVC activity. Updating PCs via entorhinal cortex (EC) GC inputs allows for a shift of viewpoint in imagery.

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Figure 5.  (A) Bottom-up mode of operation. Population snapshots at the moment of encoding during an encounter with a single object in a familiar spatial context. Left to right: PWb/o populations driven by sensory input project to the head-direction-modulated retrosplenial transformation circuit (RSC/TR, omitted for clarity, see Video 1 and Figure 2—figure supplement 1). The transformation circuit projects its output to BVCs and OVCs; BVCs and PRb neurons constitute the main drive to PCs; perirhinal (PRb/o) neurons are driven externally, representing object recognition in the ventral visual stream. At the moment of encoding, reciprocal connections between PCs and OVCs, OVCs and PRo neurons, PCs and PRo neurons, and PRo neurons and current head direction are learned (see Figure 3D). Right-most panels show the agent in the environment and the PC population snapshot representing current allocentric agent position. (B) Top-down mode of operation, after the agent has moved away from the object (black triangle, right-most panel). Current is injected into a PRo neuron (bottom right of panel), modelling a cue to remember the encounter with that object. This drives PCs associated to the PRo neuron at encoding (dashed orange connections show all associations learned at encoding). The connection weights switch globally from bottom-up to top-down (connections previously at 5% of their maximum value now at 100% and vice versa; orange arrows). PCs become the main drive to OVCs, BVCs and PRb neurons. BVC and OVC representations are transformed to their parietal window counterparts, thus reconstructing parietal representations (PWb/PWo) similar to those at the time of encoding (compare left-most panels in A and B). That is, the agent has reconstructed a point of view embodied by parietal window activity corresponding to the location of encoding (red triangle, right-most panel). Heat maps show population firing rates frozen in time (black: zero firing; white: maximal firing). DOI: https://doi.org/10.7554/eLife.33752.008
Figure 6. Firing fields of object vector cells. (A) Firing rate maps for representative object vector cells (OVCs), firing for objects with a fixed allocentric location and direction relative to the agent. Object locations superimposed as green circles. Note that the objects have different identities, which would be captured by perirhinal neurons, not OVCs. Compare to Figure 4 in Deshmukh and Knierim, 2013. White lines point from objects to firing fields. Red dotted line added for comparison with B. (B) Distribution of the objects in the arena and an illustration of a possible agent trajectory.

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Figure 7. Papez’ circuit lesions. (A) In the bottom-up mode of operation (perception), a lesion to the head direction circuit removes drive to the transformation circuit and consequently to the boundary vector cells (BVCs) and object vector cells (OVCs). A perceived object (present in the egocentric parietal representation, PWo) cannot elicit activity in the MTL and thus cannot be encoded into long-term memory, causing anterograde amnesia. Place cells fire at random locations, driven by perirhinal neurons. (B) For memories of an object encountered before the lesion, place cells can be cued by perirhinal neurons, and pattern completion recruits associated OVC, BVCs and perirhinal neurons, but no meaningful representation can be instantiated in parietal areas, preventing episodic recollection/imagery (retrograde amnesia for hippocampus-dependent memories).

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Figure 8. Correlation of neural population vectors between recall/imagery and encoding. (A) In the intact model, OVCs and place cells exhibit correlation values close to one, indicating faithful reproduction of patterns. (B) Random neuron loss (20% of cells in all populations except for the head direction ring). (C) The effect of firing rate noise. Noise is also applied to all 20 retrosplenial transformation circuit sublayers (as is neuron loss; correlations not shown for clarity). Firing rate noise is implemented as excursions from the momentary firing rate as determined by the regular inputs to a given cell (up to peak firing rate). The amplitudes of perturbations are normally distributed (mean 20%, standard deviation 5%) and applied multiplicatively at each time step. White bars show the correlation between the neural patterns at encoding vs recall (RvE), while black bars show the average correlation between the neural patterns at recall vs pattern sampled at random times/locations (here every 100 ms; RvRP). Each bar is averaged over 20 separate instances of the same simulation (with newly drawn random numbers). Error bars indicate standard deviation across simulations.

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Figure 9. Detection of moved objects via OVC firing mismatch. (A) Two objects are encoded from a given location (left). After encoding, object one is moved further North. When the agent returns to the encoding location, the perceived position of object one differs from that at encoding (blue line, middle panel). When the agent initiates recall (right) the perceived location of object 1 (green filled circle) and its imagined location (end point of blue line) differ. (B) PC activity is the same in all three circumstances, that is PC activity alone is insufficient to tell which object has moved. (C-D) The perceived location as represented by OVCs during perception (C; objects 1 and 2 sampled sequentially at times T1, T2) and during recall (D; objects 1 and 2 sampled sequentially at times T3, T4). Blue circle in panel D indicates the previously perceived position of object 1. Inset bar graphs show the concurrent activity of perirhinal cells (PRo). (E) The mismatch in OVC firing results in near zero correlation between encoding and recall patterns for object 1 (black bar), while object 2 (white bar) exhibits a strong correlation, so that object one would be preferentially explored. Note, the correlation for object two is less than 1 because of the residual OVC activity of the other object (secondary peaks in both panels in D, driven by learned PC-to-OVC connections). (F) A hippocampal lesion removes PC population activity, so that OVC activity is not anchored to the agent’s location at encoding. (G-H) An incidental match between learned and recalled OVC patterns can occur for either object at specific locations (red arrow heads in second panel in G), but otherwise mismatch is signaled for both objects equally and neither object receives preferential exploration.

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Figure 10. ‘Top-down’ activity and ‘trace’ responses. (A) An environment containing a small barrier (red outline) has been encoded in the connection weights in the MTL, but the barrier has been removed before the agent explores the environment again. (B) Activity snapshots for PWb (B1), BVC (B2) and PC (B3) populations during exploration. The now absent barrier is weakly represented in parietal window activity due to the periodic modulation of top-down connectivity during perception, although ‘bottom-up’ sensory input due to visible boundaries still dominates (see main text). (C1) High gain for top-down connections yields BVC firing rate maps with trace fields due to the missing boundary. Left: BVC firing rate map. Right: An illustration of the BVC receptive field (teardrop shape attached to the agent at a fixed allocentric direction and distance) with the agent shown at two locations where the cell in the left panel fires maximally. (C2) Same as C1 for a cell whose receptive field is tuned to a different allocentric direction. (D1) Similarly to the missing boundary in A, a missing object (small red circle) can produce ‘trace’ firing in an OVC (D2). Every time the agent traverses the location from which the object was encoded (large red circle in D1), learned PC-to-OVC connections periodically reactivate the associated OVC. (D3) The same PCs also re-activate the associated perirhinal identity cell (PRo), yielding a spatial trace firing field for a nominally non-spatial perirhinal cell (red circle). DOI: https://doi.org/10.7554/eLife.33752.021
Figure 11. Inspecting scene elements in imagery. The agent encounters two objects. (A) Activity in PWo (left) and OVCs (right) populations when the agent is attending to one of the two objects during encoding. Both objects are encoded sequentially from the same location (time index 0.22 in Video 11). The agent then moves past the objects. (B) Imagery is engaged by querying for object 1, raising activity in corresponding PRo neurons (far right) and switching into top-down mode (similar to Simulation 1.0, Figure 5 and Video 2), leading to full imagery from the point of view at encoding. Residual activity in the OVC population at the location of object 2 (encoded from the same position, that is driven by the same place cells) translates to weak residual activity in the PWo population. (C) Applying additional current (i.e. allocating attention) to the PWo cells showing residual activity at the location of object 2 (leftmost blue arrow) and removing the drive to the PRo neuron corresponding to object 1 (because the initial query has been resolved) leads to a build-up of activity at the location of object two in the OVC population (blue arrow between PWo and OVC plots). By virtue of the OVC to PRo connections (blue between OVC and Pro plots), the PRo neuron for object two is driven (and inhibits PRo neuron 1, right-most blue arrows). Thus, the agent has inferred the identity of object 2, after having initiated imagery to visualize object 1, by paying attention to its egocentric location in imagery.

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Figure 12. Mental navigation with grid cells. Left to right: allocentric agent position (black triangle) and recent trajectory (black dashed line); PWo, OVC, and PC population snapshots; GC input to PCs (i.e. GC firing rates multiplied by connection weights from GCs to PCs); PRo neurons. The rightmost panel indicates which objects have been encoded. (A) The agent is exploring the environment and has just encoded the second object into memory (right-most bar chart). Object one has been encoded near the start of the trajectory. (B) After encoding the third object and moving past it, the agent initiates imagery, recalling object one in its spatial context (top-down mode) from a point of view West of object 1, facing East (red triangle). (C) Mock motor efference shifts GC activity (dashed arrow on GC input to PCs) and thence drives the PC activity bump representing (imagined) agent location. The allocentric (BVCs) and egocentric (PWb) boundary representation follow suit (see main text and Video 12). As the PC activity bump passes the location at which object 3 was encoded, corresponding OVC activity is elicited by learned connections (and is transformed into PWo activity (solid orange arrows indicate GCs updating PCs, PCs updating OVCs, etc). NB object 3 appears in the reconstructed scene ahead-right of the agent (PWo snapshot, second panel), despite being encoded ahead-left of the agent when it moved southwards from object 2 toward object 3. The corresponding perirhinal neuron is also driven to fire by PCs (orange arrow in PRo panel).

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Figure 13. Planning, taking and imaging a trajectory across an unexplored area. The agent is located in an environment where the direct trajectory between two salient locations (purple dots, left column) covers an unexplored part of the environment. PCs potentially firing in the unexplored area (‘reservoir cells’) receive only random connections from GCs (see unstructured grid cell input in column 5). Left to right panel columns: allocentric agent position (triangle); PWb, BVC, PC population rates; GC inputs to PCs (see Figure 12); and (B-D only) firing of ‘reservoir’ PCs along the trajectory (x axis), stacked and ordered by time of peak firing along the trajectory (y axis). (A) Starting situation. (B) Phase 1; imagined movement across the obstructed space leads to preplay-like activity in reservoir PCs (rightmost panel). Red arrow indicates the reservoir PCs are driven by grid cells. No egocentric representation can be generated from BVCs because ‘reservoir’ PCs have no connections to BVCs, that is they are not yet part of the MTL attractor. (C) Phase 2; the barrier is removed and the agent navigates the trajectory in real space. GCs again drive PCs (thick grey arrow), so the temporal sequence of reservoir cell activity in (A) is recapitulated in the spatial sequence of PC activity. Sensory inputs drive the PW (bottom-up mode) and hence BVCs (grey arrow between panels 2 and 3). Hebbian learning proceeds between PCs and BVCs (dashed grey line), and from GCs to PCs (reinforcing the drive from GCs to PCs, grey arrow between panels 4 and 5). (D) Phase 3; having traversed the novel part of the environment, the agent initiates imagery and performs mental navigation along the newly learned trajectory. The learned connections now instantiate the correct BVC and PW activity in top-down mode (orange arrows indicating flow of information, similar to Figure 12).

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