How sturdy is your memory palace? Reliable room representations predict subsequent reinstatement of placed objects

Rolando Masís-Obando[1,4*], Kenneth A. Norman[1,2] and Christopher Baldassano[3]

[1*]Princeton Neuroscience Institute, Princeton University, Princeton, NJ, USA.
[2]Department of Psychology, Princeton University, Princeton, NJ, USA.
[3]Department of Psychology, Columbia University, New York, NY, USA.
[4]Psychological & Brain Sciences, Johns Hopkins University, Baltimore, MD, USA.

*Corresponding author(s). E-mail(s): rmasis@princeton.edu;

Abstract

Our autobiographical experiences typically occur within the context of familiar spatial locations. When we encode these experiences into memory, we can use our spatial map of the world to help organize these memories and later retrieve their episodic details. However, it is still not well understood what psychological and neural factors make spatial contexts an effective scaffold for storing and accessing memories. We hypothesized that spatial locations with distinctive and stable neural representations would best support the encoding and robust reinstatement of new episodic memories. We developed a novel paradigm that allowed us to quantify the within-participant reliability of a spatial context ("room reliability") *prior to* memory encoding, which could then be used to predict the degree of successful re-activation of item memories. To do this, we constructed a virtual reality (VR) "memory palace", a custom-built environment made up of 23 distinct rooms that participants explored using a head-mounted VR display. The day after learning the layout of the environment, participants underwent whole-brain fMRI while being presented with videos of the rooms in the memory palace, allowing us to measure the reliability of the neural activity pattern associated with each room. Participants were taken back to VR and asked to memorize the locations of 23 distinct objects randomly placed within each of the 23 rooms, and then returned to the scanner as they recalled the objects and the rooms in which they

appeared. We found that our room reliability measure was predictive of object reinstatement across cortex, and further showed that this was driven not only by the group-level reliability of a room across participants, but also the idiosyncratic reliability of rooms within each participant. Together, these results showcase how the quality of the neural representation of a spatial context can be quantified and used to 'audit' its utility as a memory scaffold for future experiences.

Keywords: spatial context, memory palace, reinstatement, MVPA

1 Introduction

Many of our memories are intrinsically tied to the locations where they occurred. Thinking about (or actually revisiting) places from our past can immediately bring to mind the meaningful events that occurred there. In this way, our spatial memories can serve as a map not only of physical spaces but also of our remembered experiences in those spaces. In what ways can a spatial context serve as a scaffold for storing and accessing the details of past episodes? Are there spatial contexts that are more or less effective for attaching event memories, and can we neurally measure the usefulness of a location as a memory cue even before an event has occurred?

Decades of research have found that the representation and retrieval of episodic memories is profoundly tied to spatial location. Prior behavioral research on the context-dependent memory effect suggests that items learned in a particular physical context can be better remembered when the retrieval context matches the encoding context (Smith and Vela, 2001; Godden and Baddeley, 1975), even for contexts that are experienced only through virtual reality (Shin, Masís-Obando et al., 2021) or that are mentally reinstated rather than physically re-experienced (Bramao et al., 2017). Recent behavioral work has also suggested a privileged role for spatial contexts as cues for memory retrieval. For example, spatial context cues: *a)* may enhance episodic recall when compared with temporal, thematic (e.g., romantic experience), person, or objects cues for imagined or real autobiographical memories (Sheldon et al., 2019; Robin et al., 2016; Sheldon and Chu, 2017; Sheldon et al., 2019); *b)* are spontaneously generated even when not cued by experimenters (Robin et al., 2016; Hebscher et al., 2018), sometimes leading to quicker access to episodic information (Robin et al., 2016; Hebscher et al., 2018, but see Robin et al., 2019); *c)* are associated with richer episodic memory when highly familiar to participants (Arnold et al., 2011; Robin and Moscovitch, 2014, 2017; Robin et al., 2016; Hebscher et al., 2018); and *d)* are associated with preserving long-term recollection of initially low detail memories for both young and older adults (Chang et al., 2024). This behavioral work is complemented by neuroimaging studies of autobiographical memory showing that spatial contexts have a strong influence on the neural representations of remembered or imagined autobiographical events (Robin et al., 2018; Hebscher et al., 2018; Reagh and Ranganath, 2023, among others; for a review see Hassabis and Maguire, 2007). The networks associated with spatial contexts are maintained during multiple phases of memory retrieval, possibly

acting as a scaffold for accessing additional event details (Gurguryan and Sheldon, 2019).

Despite the centrality of spatial context in memories, it is unknown whether *(a)* some specific spatial locations are more effective memory cues than others, and if so *(b)* whether this is related to properties of their neural representation. In general, two requirements for robust representation of a memory are thought to be stability over time (allowing for faithful reactivation of the features of the original experience) and distinctiveness (to prevent interference with other similar memories; Sommer and Sander, 2022; Konkle et al., 2010). We hypothesized that these two properties would also be important specifically for building an effective spatial context scaffold – i.e., that spatial locations with more stable and distinctive representations would support better encoding of new information encountered in these locations, and allow for easier access to this information at retrieval. This implies that having a stable and distinctive neural representation for a location *before* associating an object to that location will be predictive of subsequent reinstatement for that object representation, in response to the location cue. To test this idea, we custom-built a virtual reality "memory palace" environment of 23 distinct rooms that participants explored using a head-mounted virtual reality display (**Fig 1**). After participants learned the layout of the virtual environment, we used fMRI to compute a neural *room reliability* score for each of the 23 rooms. This score reflected both the stability and distinctiveness of neural representations, measuring the degree to which repeated presentations of a room evoked patterns that were more similar to each other than to patterns evoked by other rooms. Participants then returned to the VR environment, where they observed (and were asked to memorize) a new salient object that had now been placed into each room. Finally, they performed recall tasks for these items in the fMRI scanner. Overall, our results confirmed our hypothesis: Room reliability, measured before any room-object pairing occurred, predicted the degree of object reinstatement during guided and free recall, showing that it is possible to neurally diagnose whether a room will serve as an effect memory scaffold, *before* objects are placed in the room.

2 Results

2.1 Overview

How effective are spatial memory representations as containers for subsequently-bound objects? We sought to answer this question by using the reliability of a pre-learning room representation to predict the degree of reinstatement evidence for recalled objects during self-paced guided and free recall. To do this, we needed to quantify **1)** the reliability of a room representation, and **2)** the reinstatement of object information during recall. We defined room reliability as the similarity of a room representation to itself (i.e., stability) minus its average similarity to every other room (i.e., distinctiveness); importantly, this was measured before any room-object associations had been formed (i.e. in the pre-learning phase; see **Fig 2**). Our strategy for quantifying object reinstatement during recall was as follows: We first identified a network of regions involved in the retrieval of objects (the Retrieved Object Classifier Network;

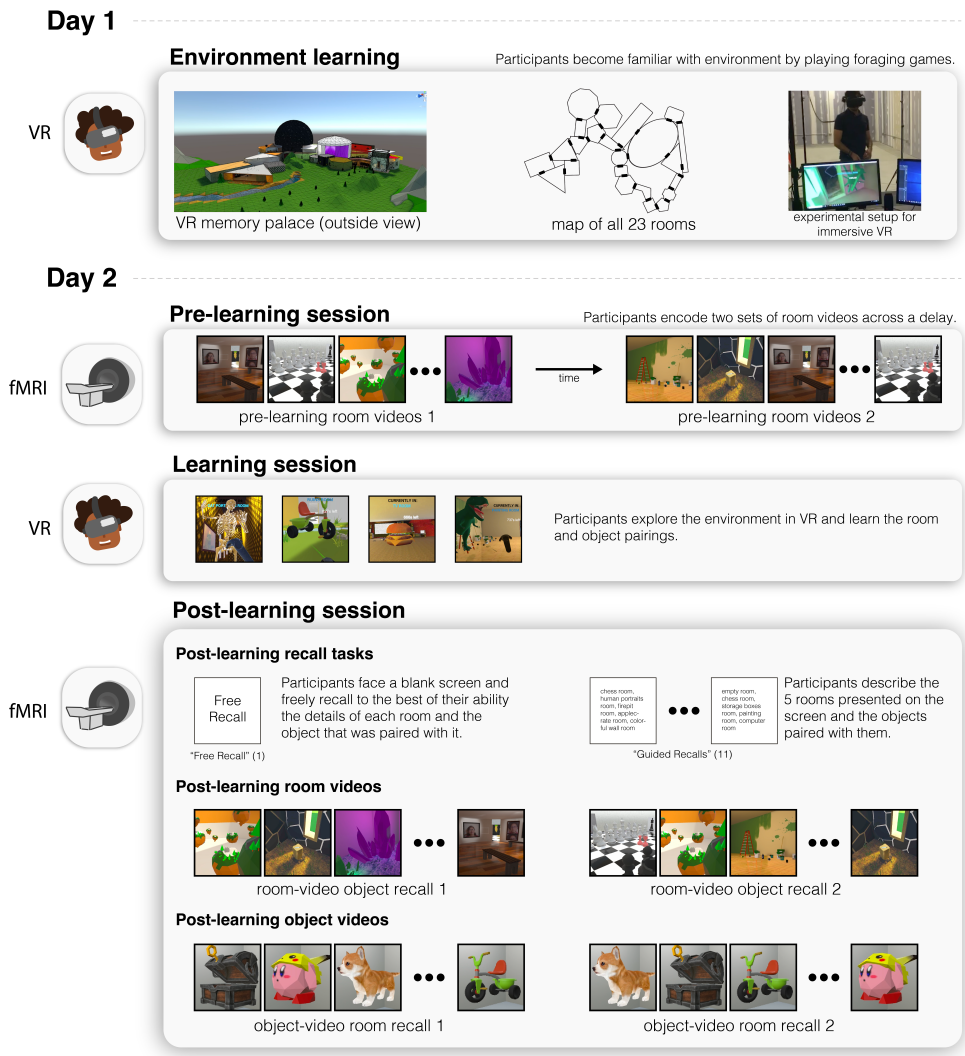

Fig. 1 Experimental paradigm. Participants played a set of foraging games to learn the layout of the 23-room virtual reality environment (photograph of a lab member demonstrating the VR setup used with permission). 24 hours later, participants were shown room videos in the scanner, with each room presented twice. Participants then re-entered immersive VR, and were given 15 minutes to learn the identities and locations of 23 new objects that had been added to the environment, one per room. Finally, participants returned to the scanner and recalled the items they had seen in a free recall task, a guided recall task (in which they recalled items along specific five-room paths), and a room video task (in which they recalled the item for each presented room). They were also presented with videos of each object, and attempted to recall the room in which each object appeared.

Figure 1–Figure supplement 1. Example bird's-eye-view drawings from a single selected participant.

ROCN) during a cued-recall task in which participants watched videos of room interiors and were asked to recall the objects that had been randomly assigned to those rooms in VR (see **Fig 3**). We then measured the average classifier evidence for object reinstatement within this network during self-paced guided and free recalls, in which participants were instructed to verbally describe with as much detail as possible the rooms and the randomly placed objects in them (see **Fig 4A**). Afterwards, to determine how well the reliability of a pre-learning room representation predicted object reinstatement, we correlated pre-learning room reliability scores with object classifier evidence within the ROCN during both self-paced recall trials (see **Fig 4B** and **Fig 5**). We identified a set of regions whose pre-learning room reliability was predictive of object reinstatement across both recall tasks, including precuneus, right retrosplenial cortex (RSC), and several regions surrounding lateral visual cortex. Importantly, using a model comparison analysis, we also found that some of these regions provided a participant-specific predictive benefit, including superior parietal cortex (SPL) and posterior middle temporal cortex (see **Fig 5C** and **Fig 5D**).

2.2 Room reliability

To identify brain regions with reliable room representations for every participant, we compared the similarity of a room's representation across runs to its similarity with representations of other rooms (**Fig 2A**). We ran this analysis on searchlights and hippocampal regions of interest (ROIs; full hippocampus, anterior hippocampus, and posterior hippocampus). We found significant room reliability across most of the cortex, with the highest reliability scores in auditory cortex, visual cortex, precuneus, and posterior hippocampus (**Fig 2C**).

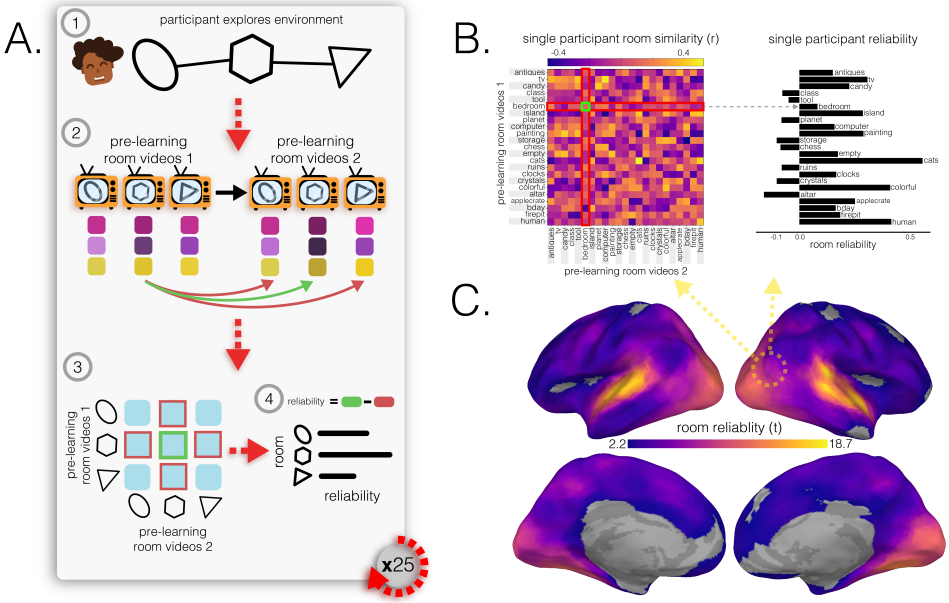

Fig. 2 Room reliability. (A.) Illustration of room reliability methodology. *(1)*: Participants first explored the memory palace in immersive VR and learned its spatial layout by playing a foraging game. *(2)*: In the pre-learning scanning session, before learning room-object pairings, participants watched and listened to videos of each room twice (pre-learning room videos 1 & 2). Each room representation was correlated across runs with every other room, in a searchlight analysis. *(3)*: Room reliability was computed by taking the difference between the similarity of a room pattern to itself (green) and the average similarity of the room with every other room (red). *(4)*: Room reliability was computed for every room, leaving a room reliability score for each of the 23 rooms. The entire procedure outlined in **A** was computed for every participant such that for every searchlight, there were 23 room reliabilities for each of the 25 participants. **(B.)** An example room pattern similarity matrix for one participant, in the searchlight denoted with a dotted circle. This matrix was used to extract room reliability scores as described in **A**, such that for each room (row), the average room similarity to other rooms (red) was subtracted from the room similarity to itself (green). **(C.)** Room reliability across the brain. Colored vertices on the surface indicate regions in which room reliabilities were significantly above zero at the group level ($q < 0.05$), with brighter colors indicating greater reliability.

2.3 Behavioral recall

On the second day, participants performed two types of recall tasks. During the guided recalls (GRs; 11 runs), participants were presented with the names of 5 rooms that followed a path within the virtual palace and were asked to freely recall details of the rooms and the randomly added objects. During the free recalls (FRs), participants were presented with a blank screen and were simply asked to freely recall, in as much detail as possible, the rooms and the added objects. Across both recall types, participants' recalls were at ceiling, with 92% and 76% of participants scoring higher than 90% recall accuracy for guided and free recalls, respectively.

2.4 Retrieved Object Classifier Network (ROCN)

To measure evidence of object reinstatement during self-paced (guided and free) verbal recall, we first needed to identify a network of regions that represent information about specific objects that were retrieved from memory; to select these regions in a non-circular fashion, we defined these regions using data from room-video object recall trials (**Fig 3A**). In these trials, participants viewed videos of all rooms and verbally recalled the object that had been assigned to each room as it was presented (**Fig 3A**). We used a leave-one-participant-out cross-validation procedure, whereby we made a neural template for each object based on object videos from N-1 participants, and then we used these templates to classify the (not-visibly-present) objects being recalled during room viewing in the held-out participant (**Fig 3A**). We opted for this across-participants approach (rather than classifying within-participants) because objects and rooms are confounded within participants, so room information could "leak" into training of a within-participant object classifier; this confound does not exist if training and testing are done across participants, each of whom has their own random set of room-object pairings. We used this procedure to identify the top 50 best object classifier searchlights ($\sim$3% of all searchlights) to make our Retrieved Object Classifier Network (ROCN; **Fig 3B**), which we used as a mask (**Fig 3D**) when measuring object reinstatement evidence during the guided and free recall tasks. We found that the top classifier searchlights were spread throughout cortex and included regions in anterior temporal cortex, frontal gyrus, posterior temporal cortex, posterior medial cortex, and superior parietal cortex, among others (**Fig 3C** and **Fig 3D**). We also conducted an alternative analysis in which we classified object representations while participants watched videos of objects (rather than retrieving object memories) to extract another network, the Perceived Object Classifier Network (POCN), which was entirely concentrated in early visual cortex (**Fig3 - Supp1**).

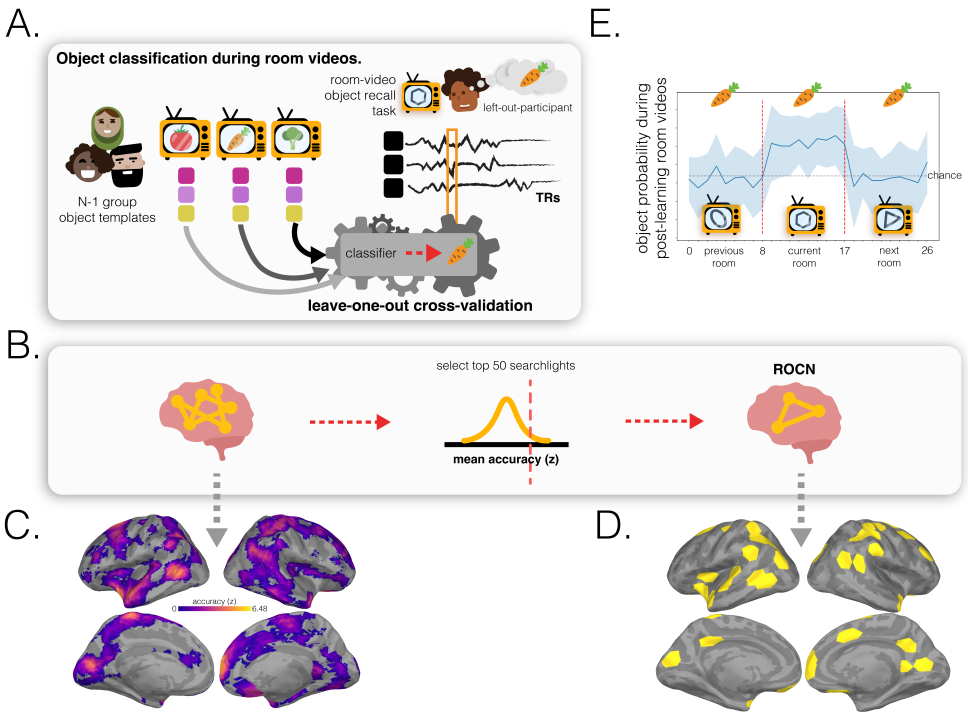

Fig. 3 Retrieved object classifier network (ROCN) methodology and surface maps. **(A.)** During the post-learning room-video object recall task, participants watched a video of a room and verbally recalled the object that was paired to it. In a leave-one-participant-out cross-validation procedure, the characteristic object patterns of the N-1 group (evoked by videos of the objects) were used to train a multinomial logistic classifier that was applied to the left-out participant's room-video object recall data. In the pictured example, the left-out participant, Fernando, is recalling the carrot object that was paired with the hexagon room currently being presented. The object classifier, trained on patterns evoked when other participants viewed the objects, was applied to each timepoint of Fernando's recall, and we measured the fraction of timepoints during the hexagon-room video that were correctly classified as activating the carrot representation. **(B.)** For each searchlight, object classification accuracies for both room-video object recall videos for each participant were averaged together and then averaged across participants and z-scored relative to a null distribution. The 50 top-performing searchlights were then selected to form the ROCN. **(C.)** Average object classification accuracy during room-video object recall. The colormap shows the relative classification accuracy across all searchlights (thresholded to show only searchlights with above-chance accuracy). **(D.)** Retrieved Object Classifier Network (ROCN). The top 50 searchlights that were most sensitive to object reinstatement (yellow) were defined as the ROCN for subsequent analyses. **(E.)** Object classifier evidence, averaged within the ROCN, for the object paired with the current room; evidence for this same object is also shown for timepoints when the previous room (associated with a different object) was being viewed and for timepoints when the next room (associated with yet another object) was being viewed. Classifier evidence for the object is above chance only when the participant is viewing the video of the room paired with that object. Error bands show the standard deviation across participants.

Figure 3–Figure supplement 1. Perceived object classifier network (POCN) methodology and surface maps

2.5 Relationship of room reliability and ROCN object reinstatement evidence

Does room reliability predict future object reinstatement during free and guided recalls? Using the object classifier and ROCN searchlights from the previous analysis, we measured the degree of object reinstatement as each participant performed free and guided recalls (**Fig 4A**). Note that using neural object reinstatement provided a more sensitive index of successful retrieval than behavioral recall accuracy, since almost all participants were near-ceiling in their retrieval accuracy as described above. Specifically, at each searchlight, we correlated each participant's room reliability with their own composite ROCN object reinstatement score (**Fig 4B**). We then averaged these correlations across participants to obtain a searchlight map (**Fig 5A** and **5B**) that indicated regions where room reliability in those regions correlated with subsequent object reinstatement (throughout the ROCN network). For both guided recalls and free recalls, notable positive relationships were observed throughout the visual cortex (extending to high-level ventral and dorsal regions), bilateral precuneus, and right retrosplenial cortex. For both guided and free recalls, notable negative relationships were observed in right anterior lateral frontal cortex and right anterior temporal cortex.

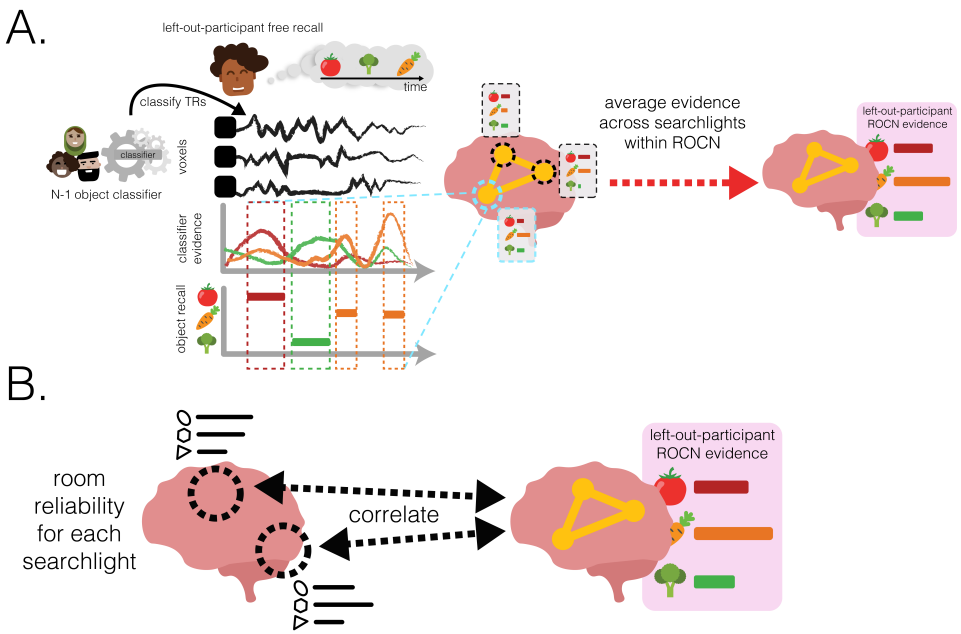

Fig. 4 Methodology for using room reliability to predict object reinstatement (A.) Illustration of methodology for how ROCN object reinstatement evidence was calculated from guided and free recalls. A leave-one-participant-out cross-validation procedure was used with a multinomial logistic classifier to predict object patterns at every timepoint of the left-out participant's recalls. To extract a single composite score of reinstatement evidence within the ROCN for every object and every participant, the classifier evidence for each object recalled was averaged within the ROCN mask across the timepoints when each object was verbally recalled. This yielded a single score for each object and each participant that represented the average object reinstatement evidence in the ROCN during guided or free recall. **(B.)** Illustration of methodology for how object reinstatement evidence was predicted by room reliability. In a searchlight analysis, reliability for a room (in that searchlight) was correlated with the corresponding composite score of reinstatement evidence (within the ROCN mask) for the object paired to that room. This correlation was computed across room-object pairs within each participant and then those correlations were averaged across participants.

To what extent do the effects in **Fig5A-B** reflect group-level differences across rooms (whereby some rooms have both high reliability and high item reinstatement in all participants) versus *participant-specific* differences in which rooms are most reliable in their individual mental maps? To answer this question, we compared the coefficient of determination between two models: 1) our original participant-specific model, where each participant's object classifier evidence was predicted using their own room reliability values, and 2) a baseline N-1 group level model, where the left-out participant's object classifier evidence was predicted using the average room reliability values from the N-1 group. We then took the regions where there was a significant participant-specific effect (i.e., better prediction with the original model), and intersected them with the correlational analysis performed in **Fig5A** and **5B**. This process revealed a participant-specific benefit of room reliability for both guided and free

recalls across the posterior middle temporal gyrus and superior parietal cortex (**Fig5C** and **5D**). Interestingly, there was also a participant-specific effect where room reliability in sparse sections of right anterior temporal cortex was negatively associated with ROCN reinstatement evidence.

In a similar fashion to how we related room reliability with object evidence within the Retrieved Object Classifier Network (ROCN), we ran a supplementary analysis in which we quantified object reinstatement within the Perceived Object Classifier Network (POCN; largely composed of visual regions) during guided and free recall (**Fig5 - Supp1**). Across participants, we found generally similar results to the ROCN results, with a positive relationship between POCN reinstatement evidence and room reliability in guided recalls and to a lesser extent in free recalls in high-level visual cortex and bilateral precuneus. For the guided recall task, there was a participant-specific benefit of room reliability in the left and right posterior middle temporal gyrus, left posterior medial cortex, left precuneus, and left anterior temporal cortex (**Fig5 - Supp1**). For the free recall task, we found a participant-specific negative relationship between subsequent object reinstatement in POCN and room reliability in left anterior temporal cortex (**Fig5 - Supp1**).

3 Discussion

In this study, we posited that a cognitive map of spatial contexts is most useful as a container for future memories when locations have reliable representations, providing specific and consistent cues every time they are accessed. To test how the neural properties of a spatial context memory supports new memories, we developed a novel paradigm that allowed us to quantify the within-participant reliability of a spatial context memory, before it became the location in which a new memory was formed, and then used it to predict the degree at which that new memory was remembered. We did this by having participants develop spatial context memories of a 23-room immersive virtual reality memory palace, scanning them to extract the neural properties of their spatial memories for "empty" rooms within the palace (pre-learning phase), and then scanning them again afterwards, as they verbally recalled the "filled" rooms and the objects that filled them (post-learning phase). For the first time, we were able to show that pre-learning room reliability – the representational quality of an "empty" memory scaffold – is predictive of post-learning object reinstatement in two types of verbal recall; we further demonstrated that – in some regions – a participant's idiosyncratic room reliability values provided a predictive advantage, beyond what could be predicted by knowing (in general) which rooms were most reliably represented across participants.

Theories in cognitive psychology have long argued that we develop knowledge structures that help to organize new information during encoding and later serve as a scaffold to recall specific details (Graesser and Nakamura, 1982); for example, prior work has discussed how event schemas (Schank and Abelson, 1977), which describe the protoypical sequence of events associated with well-learned experiences (e.g., restaurant visits), can support memory for new life events. In a similar fashion, knowledge about the structure and affordances of a spatial context can scaffold memories for

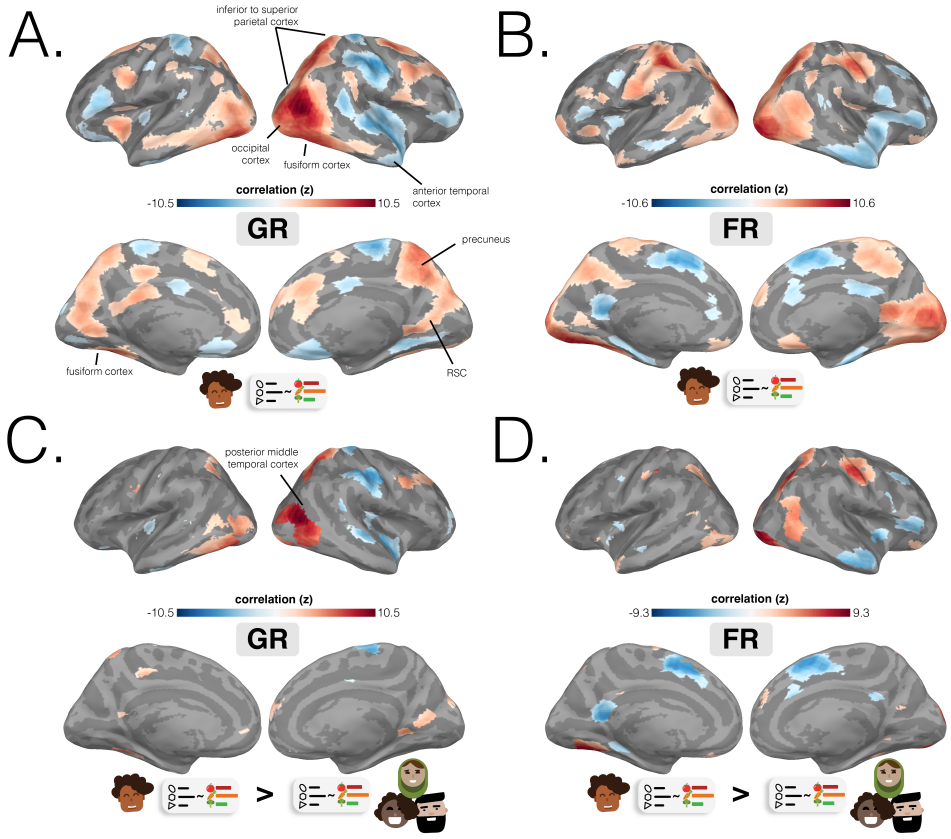

Fig. 5 Predicting ROCN object reinstatement from room reliability. **(A.)** Regions where room reliability predicted ROCN object reinstatement in guided recalls (GR). **(B.)** Regions where room reliability predicted ROCN object reinstatement in free recalls (FR). **(C.)** Regions where room reliability predicted ROCN object reinstatement in guided recalls and there was also a predictive benefit from participant-specific room reliability. **(D.)** Regions where room reliability predicted ROCN object reinstatement in free recalls and there was also a predictive benefit from participant-specific room reliability. The surface maps presented in **A** and **B** were statistically thresholded by comparing correlations to a null distribution and then FDR-correcting for $q < 0.05$. The surface maps presented in **C** and **D** show the intersection of the participant-specific models (**A** and **B**) and the regions where there was a significant positive difference in the coefficient of determination between the original participant-specific model and the N-1 group model. Statistical significance for the differences between the coefficients of determination was determined by comparing the differences to a null distribution and FDR-correcting for $q < 0.05$. All four surface maps are colored based on the magnitude of the z-scored correlation values of the participant-specific model, with blue showing negative and red showing positive relationships, respectively.

Figure 5–Figure supplement 1. Predicting POCN object reinstatement from room reliability

experiences that occur in that context (Robin et al., 2016). Our results support this general framework but also argue that all schematic containers are not equally effective at organizing memories; contexts that are only weakly learned and/or suffer interference from other contexts will not be effective scaffolds, consistent with work showing that repeated exposure to a single room versus distributed exposure to many rooms creates a more effective contextual cue (Smith, 1979).

3.1 Room reliability is predictive of object reinstatement

There are two important features that make this study uniquely placed to investigate the role of spatial context scaffolds in episodic memory. First, the virtual rooms in this study are experienced in immersive VR and vary widely along many dimensions (room size and geometry, decoration, background soundtrack, etc.), allowing participants to create rich and unique representations of individual rooms. Second, unlike other studies, neural patterns for each of the spatial contexts were acquired before the key learning event took place (here, the newly placed object in each location). These two features provided us with the opportunity to relate the neural patterns for "empty" spatial contexts with the reinstatement of the objects that had been placed in them in a subsequent part of the experiment.

Specifically, our paradigm allowed us to relate the reliability of a room representation (the "empty" scaffold) across cortex to the reinstatement of the objects that had been placed in rooms explored in VR. We found that, during both guided and free recall, object reinstatement was predicted by room reliability in precuneus, RSC, and regions throughout low and high level visual cortex (with most visible effects in the right hemisphere; **Fig 5A** and **5B**) suggesting that stable context representations are useful for retrieval regardless of how memory is cued (i.e., unaided free recall vs. guided recall). We observed strong effects in regions that are well-known to support mental and virtual navigation (Ghaem et al., 1997; Maguire et al., 1997; Hartley et al., 2003; Brodt et al., 2016; Rosenbaum et al., 2004; Ino et al., 2002; Epstein and Baker, 2019; Spreng et al., 2009), including precuneus, RSC, and the Occipital Place Area (OPA). Similar regions have also been identified in many types of tasks involving spatial knowledge: during spatially-cued retrieval of real or imagined autobiographical memories (Robin et al., 2018; Gurguryan and Sheldon, 2019; Szpunar et al., 2014), during recognition or retrieval of the spatial context in which an item was encountered (Burgess et al., 2001; Cooper and Ritchey, 2019; Hayes et al., 2004), during the recollection of spatial relationships in 2D and 3D (Frings et al., 2006; Hirshhorn et al., 2012; Schott et al., 2018; Dordevic et al., 2022), during reinstatement of spatial contexts during item retrieval (Essoe et al., 2022), and during the encoding and retrieval of items bound to a spatial context (Kondo et al., 2005; Flanagin et al., 2023).

Although these studies highlight the importance of spatial knowledge in a diverse range of learning and memory tasks, most of these studies focused on univariate or functional connectivity changes during the tasks, with few leveraging multi-voxel pattern analyses (e.g., Robin et al., 2018; Essoe et al., 2022), and none quantifying the quality of the specific spatial representations used in these tasks. Thus, our work here in combination with these prior studies, adds to the vast literature on spatial memory, and provides a potential prerequisite for the successful completion of any spatial

task: Spatial context representations need to be reliable to be useful for subsequent memory storage.

In some other brain regions, we observed that room reliability in those regions was negatively related to subsequent object reinstatement. How can we explain these negative relationships? One possibility is that these regions code for objects, not spatial contexts, and the room reliability observed in these regions was actually a measure of how strongly the background objects in those rooms (e.g., desks, chairs, posters, TVs, etc) were being represented. In this case, stronger representation of background objects (yielding higher room reliability scores) could proactively interfere with memory for the novel objects placed in those rooms (yielding lower object reinstatement scores). This might be the case for anterior temporal cortex, which is thought to specialize in object representations (Ranganath, 2010; Ranganath and Ritchey, 2012; Inhoff and Ranganath, 2017); for this region, we found a negative relationship between room reliability and object reinstatement in both recall types and both object reinstatement networks, ROCN and POCN. Further work investigating object representation in the brain and its relationship to room reliability is required to aid in parsing the negative relationships we found.

3.2 Room reliability

We described the representational stability and distinctiveness of a spatial context through a reliability score that measured the specificity of a room's representation across runs. Given that room reliability was derived from audio-visual stimuli, it was not surprising to find the strongest reliability in visual and auditory cortex. In addition to these sensory regions, we found significant room reliability in other regions that have been implicated in higher-level processing: parietal cortex (including intraparietal sulcus), posterior medial cortex (including precuneus), and lateral prefrontal cortex (including premotor cortex). In other studies, these regions have been shown to maintain specific scenes or events within stories along various time scales during movie watching (Baldassano et al., 2017; Hasson et al., 2015, 2008; Lerner et al., 2011; Masís-Obando et al., 2022). These regions may help to ensure stable and distinctive representations of the high-level properties of the current situation that go beyond low-level sensory properties — an idea consistent with prior work showing that these regions represent event-types shared across stories, regardless of whether the story is presented as an audio narrative or an audiovisual movie (Baldassano et al., 2018; Masís-Obando et al., 2022). Although some of this event structure can arise from the temporal dynamics of the stimulus itself, internal schemas can also be used to actively organize an experience into stable events (De Soares et al., 2023). Our results suggest that this kind of top-down stabilization may be most effective when the schema itself is highly reliable, providing a robust starting point for building episodic event representations.

Although high pattern similarity across identical trials is related to better subsequent memory (Xue et al., 2010), purposefully increasing variability in item encoding by varying the encoding context has been shown to improve item memory (Salan et al., 2024; Sievers et al., 2019), perhaps by increasing the number of possible retrieval cues for the item (see, e.g., Melton, 1970; Lohnas et al., 2011). It is therefore possible that

there are some situations in which *un*stable context representations would be useful for creating memories, e.g., if items are studied multiple times in a context and then recognition memory is tested in a novel context. However, in our paradigm, participants were explicitly using a context-based strategy for retrieving items, mentally simulating rooms and trajectories through rooms in order to reinstate item memories. In this case, we would expect that having a reliable contextual index for episodic memories would be critical for effective recall of items, consistent with our findings that stability in scene-related brain regions predicted item reinstatement. Future work could investigate whether this relationship disappears or reverses in other situations, such as if many items are paired with the same room (reducing the usefulness of rooms as memory cues), or if rooms had features that varied, e.g., with time of day (such that representational variability might reflect meaningful changes in contextual features).

3.3 Our experimental paradigm and the method of loci

Our "memory palace" paradigm shares some similarities with the mnemonic technique called the method of loci (MOL), in which items are associated with an *imagined* sequence of spatial locations in a pre-learned map. The motivation for this technique is related to the hypothesis tested in this study: that a well-learned spatial map consisting of many distinct locations is the optimal encoding environment for new item memories. Neuroimaging studies of this technique have largely focused on the impact of MOL (at varying levels of training or compared to other mnemonics) during item encoding (Maguire et al., 2003; Nyberg et al., 2003; Dresler et al., 2017; Wagner et al., 2021; Liu et al., 2022), with only a few performing univariate contrasts during recall (Kondo et al., 2005; Mallow et al., 2015; Fellner et al., 2016; Liu et al., 2022), and none measuring the stability of *specific* locus patterns or item reinstatement during recall. The univariate results during recall have shown enhanced engagement of regions including RSC and precuneus after instruction in MOL (Kondo et al., 2005), suggesting that spatial representations of loci are strategically activated during retrieval. It remains an open question whether the room reliability measure in our study captures the same neural mechanism engaged by MOL, but we hypothesize that locus representations would be highly reliable after training, even though these representations are internally generated rather than being evoked by an audiovisual stimulus.

4 Conclusion

After participants learned a complex spatial environment in VR, we measured the neural reliability of each spatial location within this map. When participants later used this environment to learn a new set of room-object associations, we showed that this room reliability measure could predict the degree to which objects associated with each room successfully came online during naturalistic recall. Together, these results showcase how the quality of a spatial context can be quantified and used to 'audit' its utility as a memory scaffold for future memory.

5 Methods & Materials

5.1 Participants

Data were collected from a total of 30 participants between the ages of 21–32 (16 females, 14 males) with normal or corrected-to-normal visual acuity. At the end of the study, participants were paid and debriefed about the purpose of the study. Every effort was made to recruit an equal number of female and male participants and to ensure that minorities were represented in proportion to the composition of the local community. The experimental protocol was approved by the Institutional Review Board (IRB) of Princeton University, and all participants provided their written informed consent (IRB #7225). Due to technical difficulties (corrupted and missing files), 5 participants were excluded, leaving a total of 25 participants (11 females, 14 males).

5.2 Stimuli

5.2.1 Virtual reality stimuli

Environment: A custom-built virtual reality environment made up of 23 interconnected distinct rooms with distinct soundtracks was explored by participants using a head-mounted virtual reality display. Each of the rooms was built to be as visually and aurally distinct as possible. To that end, for visual distinctiveness, each room followed a different theme (e.g., planetarium, computer store, etc) with theme-congruent objects carefully placed throughout, and the rooms had different shapes (e.g., oval, rectangle, etc) and different sizes (e.g., large, small, etc). To promote auditory distinctiveness, each room had a distinct soundtrack on loop that was audible only when a participant entered each room and some rooms contained specific sound effects that matched the room context (e.g., bird chirps if the room had a window facing the outside).

The majority of rooms were connected with only 2 other connecting rooms, while a few, 'hubs', had more than 2 connecting rooms. Of all 23 rooms, 16 rooms (70%) were connected with 2 other rooms, 6 rooms (26%) were connected with 3 other rooms, and 1 room (4%) was connected with 4 other rooms.

To reduce the potential for motion sickness, participants explored the virtual world while seated in a 360 degree rotatable chair, and any instance of participant-initiated teleportation was followed by a short and smooth fade-in-and-out of black. Participants teleported within and between rooms by pressing a button on a wireless controller that would appear digitally reconstructed in VR as a 3D object. The range of teleportation was limited to force teleportation across small distances and to avoid fast teleportation across rooms. Rooms were connected by doorways; given the current room a participant was in, only the immediately connected rooms were visually accessible via the doorways, while further-away rooms were culled from view.

Music and Sounds: Sounds of birds, ambience, firewood crackling, and others, were manually recorded or freely downloaded from the internet. Music for each room was either custom-composed in Ableton Live software, downloaded from the internet, or requested from professional composers (**Supplementary Table 1**).

All tasks were presented on a wired HTC Vive head-mounted display (1,080 × 1,200 resolution per eye, with a 90-Hz refresh rate, and built-in headphones and integrated

microphone), which was connected with a wire to a computer running 64-bit Windows 10 on an Intel Core i7-6800K CPU @ 3.40GHz with 32GB RAM and an Nvidia GeForce GTX 1080 graphics card.

All tasks and visual presentations were created and coded in Unity3D 5.5.2f1 (and 2017.1.2f1), a game-development platform, with Virtual Reality Toolkit (VRTK; vrtk.io), a virtual-reality programming tool-kit for Unity3D. The majority of 3D models, textures, environments and other assets were custom-built using SketchUp (sketchup.com) or Blender (blender.org). The remaining assets were downloaded from the Unity Asset Store (assetstore.unity.com), Turbosquid (turbosquid.com), or other publicly available online repositories, and then modified using Blender to reduce model complexity and size.

5.2.2 Scanning stimuli

During scanning, participants were presented with videos of rooms and videos of objects. These videos were generated beforehand and presented to participants in a pseudorandom order.

Room videos: To generate the room videos using Unity, a virtual camera was placed in the center of each room. The camera was scripted to rotate a full 360 degrees to capture the panorama of each room within 10s. OBS Studio (obsproject.com) was used to screen capture the output of the virtual camera. Each room video lasted 10s and was followed by a 5s interstimulus interval before the next video.

Object videos: To generate the object videos, a virtual photography studio was created with a blank backdrop and a 3 point lighting setup. All 23 objects were placed in the center of the virtual studio and scripted to rotate 360 degrees in front of a virtual camera facing them within 10s. OBS studio was used to screen capture the output of the virtual camera. Similarly to the room videos, each object video lasted 10s and was followed by a 5s interstimulus interval before the next video.

Stimulus presentation: All generated stimuli were presented to participants in the scanner using PsychoPy (Peirce, 2007) to time task and stimulus presentations with the scanner trigger. Every presented video or task instruction was preceded by a 5s black screen.

5.3 Data acquisition and pre-processing

5.3.1 MRI acquisition & pre-processing

MRI data were collected on a 3T full-body scanner (Siemens Prisma) with a 64-channel head coil. Functional images were acquired using an interleaved multiband EPI sequence (TR = 1300ms, TE 33ms, flip angle 80 degrees, whole-brain coverage, 2 mm slice thickness, FOV 192 mm^2, SMS = 4). Anatomical images were acquired using a T1-weighted magnetization-prepared rapid-acquisition gradient echo (MPRAGE) pulse sequence (1 mm^3 resolution). Anatomical images were acquired in a 6-min scan before the functional scans; during this scan, participants watched videos of paragliding from YouTube. Field maps were collected but not used in our preprocessing pipeline.

All raw data acquired from MRI were converted to BIDS formatting (BIDS version 1.0.1), anatomical images were de-faced using pydeface (version 2.0.0), and resulting

data were subsequently preprocessed using fMRIPrep version 1.0.3, a Nipype (Gorgolewski et al., 2011, 2017) based tool. Each T1w (T1-weighted) volume was corrected for INU (intensity non-uniformity) using N4BiasFieldCorrection v2.1.0 Tustison et al. (2010) and skull-stripped using antsBrainExtraction.sh v2.1.0 (using the OASIS template). Brain surfaces were reconstructed using recon-all from FreeSurfer v6.0.0 (Dale et al., 1999), and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (Klein et al., 2017). Volume-based spatial normalization to the ICBM 152 Nonlinear Asymmetrical template version 2009c (Fonov et al., 2009) was performed through nonlinear registration with the antsRegistration tool of ANTs v2.1.0 (Avants et al., 2008), using brain-extracted versions of both T1w volume and template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast (Zhang et al., 2001) (FSL v5.0.9). Surface-based normalization based on nonlinear registration of sulcal curvature was applied using the fsaverage6 surface template from FreeSurfer.

Functional data was slice time corrected using 3dTshift from AFNI v16.2.07 (Cox, 1996) and motion corrected using mcflirt (FSL v5.0.9 Jenkinson et al., 2002). "Fieldmap-less" distortion correction was performed by co-registering the functional image to the same-participant T1w image with intensity inverted (Huntenburg, 2014; Wang et al., 2017), constrained with an average fieldmap template (Treiber et al., 2016), implemented with antsRegistration (ANTs). This was followed by co-registration to the corresponding T1w using boundary-based registration (Greve and Fischl, 2009) with 9 degrees of freedom, using bbregister (FreeSurfer v6.0.0). Motion correcting transformations, field distortion correcting warp, BOLD-to-T1w transformation and T1w-to-template (MNI) warp were concatenated and applied in a single step using antsApplyTransforms (ANTs v2.1.0) using Lanczos interpolation.

Physiological noise regressors were extracted applying CompCor (Behzadi et al., 2007). Principal components were estimated for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). A mask to exclude signal with cortical origin was obtained by eroding the brain mask, ensuring it only contained subcortical structures. Six tCompCor components were then calculated including only the top 5% variable voxels within that subcortical mask. For aCompCor, six components were calculated within the intersection of the subcortical mask and the union of CSF and WM masks calculated in T1w space, after their projection to the native space of each functional run. Frame-wise displacement (Power et al., 2014) was calculated for each functional run using the implementation of Nipype.

5.3.2 Additional pre-processing

After fMRI data were aligned and preprocessed to fsaverage6 resampling, the resampled data were further preprocessed with a custom Python script that removed nuisance regressors which included the 6 degrees of freedom motion correction estimates; framewise displacement: the estimated bulk-head motion; head motion estimates from white matter and CSF, and the cosine bases for high pass filtering to account for low-frequency signal drifts (up to 0.008 Hz, or 125 seconds). Within the

same python script, the resulting timeseries data was z-scored for each run (i.e,. task), such that there was a single preprocessed timeseries per task (e.g., pre-learning room videos, post-learning object videos, recall, etc).

5.4 Experimental paradigm

The study took place on two consecutive days and was composed of a behavioral session on day 1 and a behavioral and two scanning sessions on day 2.

Day 1

On day 1, participants were familiarized with the virtual environment and exposed to two VR foraging games and hand-drawing tasks to facilitate the learning of the spatial layout. Specifically, on day 1, after participants read and signed the consent and screening documents, participants were informed about what they would be experiencing in VR and about the safety measures taken to ensure their safety and comfort. They were told that they would be seated to decrease potential dizziness that arises more commonly during VR that involves standing. They were also informed that at any time the experiment could be stopped if they are feeling uncomfortable or dizzy. They were told that they would play two foraging games in virtual reality that involve freely moving through the virtual reality environment with the goal of collecting floating cubes. In the first game they had to collect a cube from every room. In the second game they had to repeatedly navigate to designated rooms to collect additional cubes. They played the second game twice. Between each game, participants were asked to draw a bird's-eye-view map based on their current knowledge of the environment (**Fig1 - Supp1**) – we did this to ensure participants were learning the spatial layout of the environment. By the end of the behavioral session participants had completed a total of three games and three maps. Throughout the experimental session, the experimenter asked the participant about their overall comfort and reminded them if they feel dizzy or nauseous, the experiment could be easily stopped without consequence. After the completion of the foraging tasks, the participants were compensated and reminded to return the next day for the two scanning sessions and the additional VR behavioral session.

Day 2

On Day 2 (1 day later), three sessions took place: In the first session, participants were scanned with fMRI for a small battery of encoding tasks (pre-learning scan); in the second session, participants learned room-object associations in VR for randomly placed objects in each of the 23 rooms (learning behavioral session), and in the third session, participants were scanned again with fMRI as they proceeded through a battery of encoding and retrieval tasks (post-learning scan).

Session 1 (pre-learning scan): On day 2, participants were greeted at the MRI room, asked to draw a bird's-eye-view map of the environment (as had been done the day before). After listening to a short unrelated audio clip in the scanner to verify volume level, participants were told that they would be presented with two sets of audiovisual stimuli of the rooms. In the first set they saw 360-degree room rotation videos of all the rooms (i.e., pre-learning room videos) and were instructed to verbally recall the name of the room when they recognized it. The second set, which was viewed

after the first, was exactly the same as the first, except room order was randomized for each participant. Every stimulus presentation was preceded by a 5s blank screen.

Session 2 (learning behavioral session): After participants finished the pre-learning scan, they were taken out of the scanner bore and instructed to carefully stand up. They were then guided back to the behavioral room with the VR equipment to complete the second session of VR. In this session, participants were refamiliarized with the environment by playing the first foraging game again. Afterwards, they drew a bird's eye view map once again and then were told that when they returned to the virtual world, they would find 23 different 3D objects scattered in each of the 23 rooms. They were then given 15 minutes to memorize the room-object pairings.

Session 3 (post-learning scan): After the 15 minutes that participants were given to memorize the room-object pairings had elapsed, participants were guided back into the MRI room. Before getting into the scanner, participants were told that they would be asked to verbally recall in as much detail as possible the 23 room-object pairings. They were also told that they would be presented with the same audiovisual stimuli from Session 1, and they would also view an additional set of videos that included objects. In the first task (Free Recall), participants were asked to describe in as much detail as possible all the rooms and objects that they saw in VR. In the second task (Guided Recall), participants were asked to recall with as much detail as possible the appearance of the rooms and objects along specific 5-room paths within the environment. The names of the 5 rooms were visible on screen. They did this guided recall task 11 times, each time with a different 5-room path. When they had completed recalling the rooms and objects to the best of their ability for the Free Recall and Guided Recall tasks, they were told to inform the experimenter by saying "Done". In the third task (which we label as room-video object recall), participants were exposed to the same 360-degree room rotation videos from the aforementioned pre-learning room video tasks, but this time when they were shown a room video, they were tasked to recall the novel object that had been placed in it (i.e., room-video object recall). They did this task twice for all rooms. Because room-object pairings were generated randomly for each participant, the objects recalled during this task were usually different across participants. Afterwards, in the fourth in-scanner task, participants saw the post-learning object videos. During these, participants performed the object-video room recall tasks: Participants were shown 360-degree object rotation videos and instructed to say the name of the room that was paired with that object. They did this task twice for all objects.

5.5 Searchlights

Our searchlights were generated by constructing them with every valid vertex as their center, then iteratively removing the most-redundant searchlights until no more could be removed while covering each vertex with at least 10 searchlights. This process yielded 1483 searchlights per hemisphere.

5.6 Hippocampus

Our full hippocampus region of interest (ROI) was extracted from a freesurfer subcortical parcellation. This ROI was then split into an anterior portion ($y > -20$) and posterior portion ($y \leq -20$) in MNI space (Guo and Yang, 2020; Poppenk et al., 2013; Masís-Obando et al., 2022).

5.7 Behavior

5.7.1 Behavioral event matrices

Pre-learning and post-learning room, and object videos: The timing of stimulus presentations for every room and object was logged, and a custom python script was used to convert the timestamps to a behavioral timeseries event matrix that marked the start and end of every stimulus presentation for every participant. The resulting matrix that contained the timing (in milliseconds) and room or object identity was then downsampled to 1.3s TRs and used in subsequent analyses to index into a participant's BOLD timeseries data to identify the moments in time participants were encoding a specific video. In sum, the python script generated 6 different behavioral event matrices, 2 pre-learning room event matrices (i.e., pre-learning room videos), 2 post-learning room event matrices (i.e., room-video object recall tasks), and 2 post-learning object event matrices (i.e., object-video room recall tasks).

Post-learning free recall and guided recall: Participants were asked to recall and describe the rooms in the virtual environment and the objects paired to the rooms. Using TotalRecall (memory.psych.upenn.edu/TotalRecall) audio files of participant's recalls were imported and transcribed by timestamping the start of a room or object verbal description. For example, if a participant said, "I remember walking through the chess room, it had large chess pieces. The object in there was a basketball..." the start and end of the "chess room" timestamps would have been at the start and end of the first sentence, respectively. This is because we assumed that the room would have come to mind at the start of the sentence rather than midway. Similarly, the object start timestamp would have been considered the start of the second sentence. For every participant, these timestamps were then imported into a custom Python script that generated a behavioral timeseries event matrix that marked the start and end of each verbal room or object recall. This resulted in 11 guided recall and 1 free recall behavioral timeseries event matrices that indicated the trajectory of room or object recalls. These were then downsampled to 1.3s TRs and used in subsequent analyses to index into a participant's BOLD timeseries data to identify the moments in time a participant was recalling a particular room or object.

5.8 fMRI analysis

5.8.1 Characteristic object patterns ("object templates")

To acquire the characteristic neural patterns for objects ("object templates") we created 23 regressors to model the neural response to each of the 23 objects. We placed each of the 23 object regressors in a design matrix that marked the transitions between object videos across both post-learning object video tasks; the matrix was convolved

with a hemodynamic response function (HRF) from AFNI (Cox, 1996) and then z-scored. We then extracted the characteristic spatial pattern across vertices for each object by fitting a general linear model (GLM; within each participant) to the time-series of each vertex using these 23 regressors. Doing this simultaneously across both post-learning object videos yielded a single set of 23 characteristic object spatial patterns across vertices for each participant. These object templates, which were obtained for every participant, were then used in subsequent analyses for training multinomial logistic classifiers.

5.8.2 Characteristic room patterns ("room templates")

To acquire the characteristic neural patterns for rooms ("room templates"), we followed the same procedure that we used for extracting object templates, but here – instead of using post-learning object videos – we used the pre-learning room videos obtained from the first scanning session on day 2 to obtain the characteristic spatial pattern across vertices for every room.

5.8.3 Room reliability

We hypothesized that, in order for a room to serve as an effective retrieval cue for associated memories (i.e., objects paired to rooms), the neural representation for that room must be stable over time and distinct from other room patterns. We captured these properties with a composite measure we called *room reliability*. Crucially, this measure was computed based on data that were collected prior to participants learning the room-object associations.

To compute room reliability, we obtained the characteristic spatial pattern for each room for each participant, using the procedure outlined above (in the **Characteristic objects patterns** section), but for room videos instead of object videos. Doing this for both pre-learning room video tasks yielded 2 sets of 23 characteristic spatial patterns across vertices (separated in time) for each participant.

We then created a room pattern similarity matrix by correlating the characteristic neural patterns for the rooms from the first pre-learning room video set with the neural patterns for the rooms from the second set. This yielded a 23 x 23 correlation (similarity) matrix for each participant. Because the two pre-learning room videos were separated by a delay, the principal diagonal indicated the similarity of the room representations over time – this was our measure of the stability of the room representations. Similarly, the off-diagonal entries indicated the similarity of one room to another over time, reflecting greater distinctiveness. To create our composite room reliability score for each room, we subtracted the average similarity of the off-diagonal entries (how similar room A is to other rooms over time) from the principal diagonal entry (how similar room A is to itself over time). A large positive difference indicated that a particular room (e.g., room A) was more similar to itself over time than it was to other rooms, indicating its stability and its distinctiveness from other rooms. We did this procedure to obtain a room reliability score for each room of each participant. To quantify significance, for each participant, we averaged reliability across all rooms to get a single difference score per vertex, and performed a 1-sample t-test on these

differences against zero before running FDR-correction on the resulting p-values and thresholding at $q < 0.05$.

5.8.4 Object classifier network selection

In order to identify which regions across the brain are involved in the retrieval of object information during guided or free recall, we first needed to identify regions across the brain that could discriminate between objects. To do this, we used two separate phases of the experiment to extract networks that could classify objects during retrieval (when perceptual details of an object were not available) and during perception (when the perceptual details of an object were available). After participants had learned the room-object associations in VR, they were scanned while they watched videos of rooms and asked to recall the objects that were in them (room-video object recall task / post-learning room videos). We used this cued-recall task to identify the retrieval networks (Retrieved Object Classifier Network; ROCN) involved in classifying objects during room videos. Similarly, we identified the networks (Perceived Object Classifier Network; POCN) involved in perception of objects, by classifying objects during post-learning object videos. Importantly, all classifiers were trained using a leave-one-participant-out procedure 25 times, where testing occurred on the left-out participant. The fact that each of the 24 participants in the training dataset had their own set of random room-object pairings ensured that the classifier was able to learn object representations that were not contaminated with room information (by contrast, if we had used a within-participant classification approach, room and object information would have been confounded, since objects were only scanned after they had been paired with a particular room).

Network selection procedure

In brief, we ran object classifiers on post-learning room videos, where participants had been asked to recall the name of the object paired to the shown room, to identify a network of regions involved in retrieving non-visible object identity. This process involved the following steps: **1)** acquiring the characteristic neural pattern for each object (post-learning object templates); **2)** using a leave-one-participant-out multinomial logistic classifier, trained on the object template patterns for the (N-1) group, to predict object identity in the excluded participant's post-learning room videos (to identify the Retrieved Object Classifier Network) or post-learning object videos (to identify the Perceived Object Classifier Network); and **3)** averaging classifier performance (i.e., accuracy) across all validation searchlights and then selecting the top 50 best classifier searchlights ($\sim$3%). This procedure was done on each searchlight plus the hippocampus ROIs for all participants. Further details are outlined below.

1) Characteristic object patterns (object templates): To extract characteristic neural patterns for objects ("object templates") we used the procedure previously described in the **Characteristic object patterns** methods section.

2) Classifier cross-validation procedure: We applied a leave-one-out cross-validation procedure to predict the left-out participant's object reinstatement at every time point during post-learning room viewing after fitting (i.e., training) a multinomial logistic classifier with the other participants' object pattern templates (i.e., the characteristic spatial patterns estimated from the GLM). More specifically, we shifted

the left-out participant's post-learning room video's BOLD timeseries by 4 TRs to approximate the HRF delay, and then trained the classifier with the other participants' object templates before predicting the object class for every timepoint of every room video. To assess the significance of classifier accuracy, we compared the classifier predictions to the correct object class labels and then generated a null distribution of accuracies by shuffling, without replacement, and while preserving their temporal contiguity, the correct object class labels 1000 times; this null distribution was used later to identify searchlights that had above chance accuracy. We did this procedure across all participants such that every participant served as a test participant.

3) Retrieved Object Classifier Network selection: Post-learning room videos were shown twice to each participant. We ran the leave-one-out cross validation procedure described in the previous section for both runs of the post-learning room viewing separately and then, across all participants and both runs, averaged the classifier accuracy including the corresponding null distributions. We then z-scored the searchlights' (and hippocampus ROIs') performance by comparing the true average accuracies to the average null distribution of accuracies. Afterwards, we extracted the top 50 ROIs with the highest z-scores. This resulted in 50 searchlights (distributed unevenly across hemispheres and excluding hippocampus) corresponding to the searchlights with the top performing classifier performance; these 50 searchlights made up the object retrieval network that we used as an ROI mask in subsequent analyses.

4) Perceived Object Classifier Network We applied the same procedure described in the **Retrieved Object Classifier Network selection** section, but instead of classifying non-visible object identity from post-learning room videos, we classified object identity from the post-learning object videos where objects were perceptually visible. In a similar fashion, we extracted the top 50 ROIs by sorting the z-score of accuracies to obtain the network involved in classifying visible objects. Unsurprisingly, the this network was focused on primary visual cortex.

5.8.5 Object evidence during guided and free recall

We used the same leave-one-out cross validation procedure described previously to predict object identity during guided and free recalls. As described previously, we shifted each recall timeseries (11 guided recalls and 1 free recall) by 4 TRs to approximate the HRF delay, and used the multinomial classifier to predict object classes at every timepoint for every participant's recalls. Given that that multiclass classifier was trained on all 23 object classes, we obtained a probability distribution across all 23 classes that described the evidence of each class being reinstated at each timepoint. For any run of a specific guided or free recall, we collected the total object evidence across all timepoints a participant verbally recalled that object, and then averaged across recall runs (guided and free recalls separately). For example, if during the first guided recall a participant verbally recalled the object "teddy bear" in two instances for a total of 16 TRs, we collected the classifier probability for "teddy bear" across those 16 TRs and then similarly for every TR "teddy bear" was recalled in all other guided recalls before averaging to get the total "teddy bear" evidence. For a given participant, we did this for each object combining across all 11 guided recalls and, separately, for the

participant's single free recall, yielding 23 mean object probabilities for each type of recall task (guided and free recall) for each searchlight.

We wanted to obtain a single value for each object in each participant (separately for guided and free recall), indicating how well that object was reinstated when participants thought about the associated room. We did this in two ways: By averaging an object probability across all searchlights that formed part of ROCN or POCN, to obtain an overall ROCN or POCN reinstatement score, respectively, for every object and every participant. We used these as our overall network object reinstatement scores in our subsequent analysis.

5.8.6 Relationship between room reliability and object reinstatement

We hypothesized that rooms with more reliable representations in the pre-learning scans would be associated with higher levels of object reinstatement during guided and free recall. To do this, we ran a searchlight analysis where we correlated the reliability of a room (see **Room reliability** methods section) with the network's evidence for the object paired to that room (see **Object classifier network selection** methods section). We did this for every room-object pair within a participant. For example, for a particular participant, the 23 room reliabilities were correlated with the 23 object reinstatement probabilities for the retrieval network. Afterwards, we averaged the correlations across participants and then, to test for statistical significance, we ran a nonparametric permutation test in which we randomly shuffled the object labels 1000 times to generate a null distribution of correlations.

5.8.7 Benefit of participant-specific room reliability

The analyses shown in **Figure 5** assess whether there is a within-participant relationship between room reliability (in a particular searchlight) and object reinstatement. Importantly, there are two possible explanations for this effect (not mutually exclusive). The first is that, within a particular participant, there are idiosyncratic differences in room reliability that predict object reinstatement for that participant – we call this a participant-specific effect. However, there is a second possible explanation: Some rooms may be more reliable than others (averaging across the whole group), and these generally more reliable rooms may support better object reinstatement on average (e.g., the chess room might consistently be better represented across people and support better object recall) – we call this a group-wise effect. Both kinds of effect are important, but they have different connotations: If the relationship between room reliability and object reinstatement is driven by idiosyncratic (participant-specific) factors, then there is predictive value in doing a "personalized audit" of the person's memory palace by scanning them; but if there is only a group-wise relationship, there is no need to collect scanning data from a new person, so long as you already have data on room reliability from the rest of the group. To assess whether the observed within-subjects relationship between room reliability and object reinstatement has a participant-specific component, we ran two ordinary least squares regressions where the current participant's object reinstatement probabilities were predicted by either

that participant's room reliability values (as in **Figure 5A** and **B**) or the average room reliability values from the N-1 group. We then ran a model comparison analysis where we took the difference between the coefficient of determination (R^2) of the participant-specific and the N-1 group models. A significant positive difference in this analysis indicates that the participant-specific model explains the variability in object evidence better than the N-1 group consensus (and thus the observed results can not be entirely due to the group-wise effect). To test for statistical significance, we ran a nonparametric permutation test where the object labels were randomly shuffled 1000 times to generate a null distribution of model performance for each model.

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7 Supplementary Information

Supplementary Table 1 Virtual memory palace room music

Room id	Room Name	Track Name	Track Artist
1	Antiques Room	Rio De Colores	Strunz & Farah
2	TV Room	Birds	Rolando Masís-Obando
3	Candy Room	Liar Liar	The Castaways
4	Classroom	Scatting at the 18th Grammy Awards, Feb. 1976	Ella Fitzgerald & Mel Tormé
5	Tool Room	brazil loops 1	motion_correct
6	Bedroom	Rero	Burne Holiday
7	Floating Islands Room	Brooks Was Here (800% slower) (Rolando Masís-Obando StretchMix)	Thomas Newman
8	Planet Room	Electric à la Mass Effect	Rolando Masís-Obando
9	Computer Store Room	Inmersión	Éditus 360
10	Painting Room	Juana y Mi Hermana	Sonámbulo Psicotropical
11	Storage Boxes Room	Aragorn's Speech at the Black Gate	from Lord of the Rings
12	Chess Room	Prelude in G Minor (Op. 23 No. 5)	Sergei Rachmaninoff
13	Empty Room	Wrong Side	Strapping Young Lad
14	Cat Portraits Room	Symphony No.8 "Unfinished" D 759	Franz Schubert
15	Ruins Room	Memory (Extended)	Nathan Prillaman
16	Clocks Room	Birds Stretched	Rolando Masís-Obando
17	Crystals Room	colorthought - crash _JR 11.4.16	Jakob Reske
18	Colorful Wall Room	Zaggazagga	Rolando Masís-Obando
19	Altar Room	Throatsinging	Rolando Masís-Obando
20	Applecreates Room	Tron Overture (form the Motion Picture TRON: Legacy)	Daft Punk
21	Birthday Party Room	Birthday Horror	Rolando Masís-Obando & the Ken Norman Lab
22	Firepit Room	fire crackles	N/A
23	Human Portraits Room	What Way?	Javier Masís

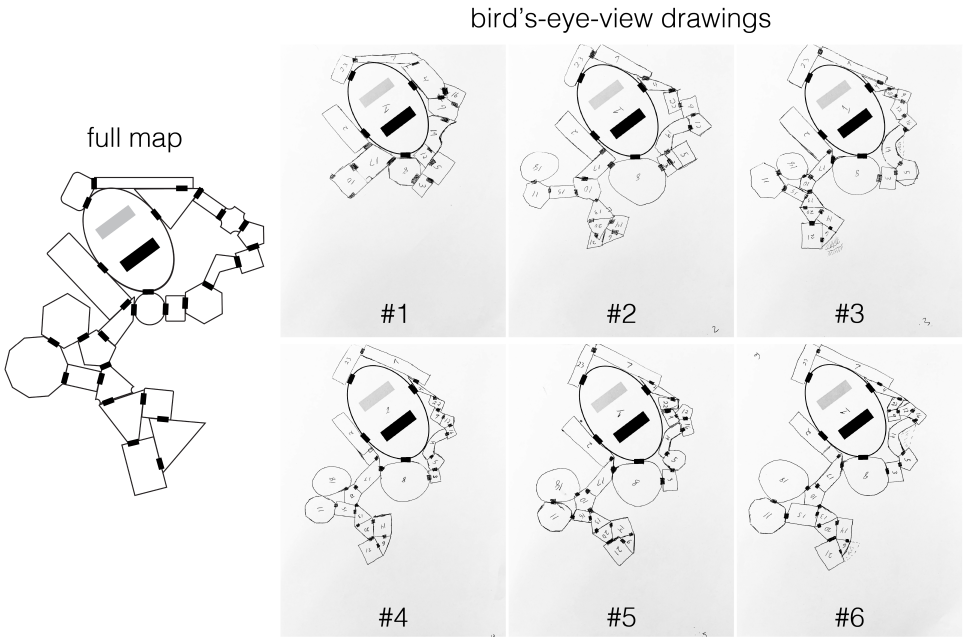

Figure 1–Figure supplement 1. Example bird's-eye-view drawings from a single selected participant. Each participant was asked to draw multiple bird's-eye-view maps of the environment across pre- and post-learning sessions to monitor training progress. Each participant was given two sheets of paper, one for the map they had to draw with a central room drawn in, and another with a legend containing the room name and pre-determined room number to facilitate map drawing and room labeling.

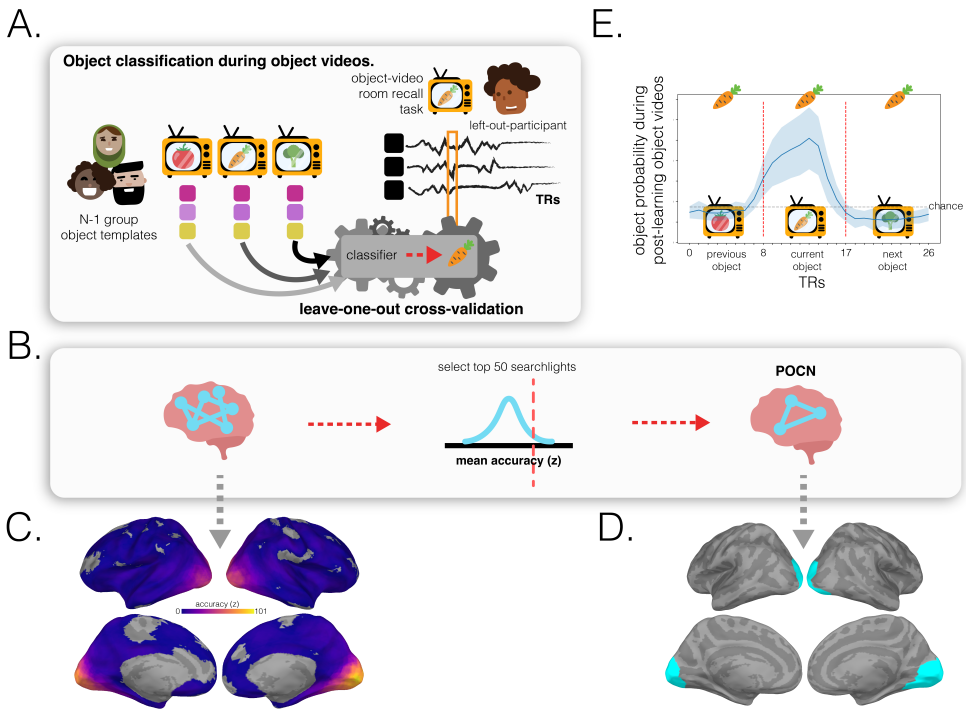

Figure 3–Figure supplement 1. Perceived object classifier network (POCN) methodology and surface maps. (A.) As for the ROCN, the characteristic object patterns of the N-1 group were used to train a multinomial logistic classifier. Here, this classifier was applied to timepoints when the left-out participant was viewing objects during the post-learning object videos, e.g. viewing a video of a carrot in this example. **(B.)** After object classification was performed for both post-learning object video runs for each participant, average classification accuracies across participants for each searchlight were then averaged across both runs and then z-scored relative to a null distribution. The top 50 searchlights were then selected to form the POCN. **(C.)** Average object classification accuracy during object encoding (thresholded to show searchlights with above-chance accuracy). **(D.)** Perceived Object Classifier Network. The surface map shows the top 50 best object classifying searchlights during both post-learning object video tasks across participants. **(E.)** Average object classifier evidence for the object that was currently being viewed, averaged within the POCN; evidence for this same object is also shown for earlier timepoints when another object was being viewed and for timepoints when the next object in the trial was being viewed. Classifier evidence for the object is above chance only when the participant is viewing the video of the matching object. Error bands show standard deviation across participants.

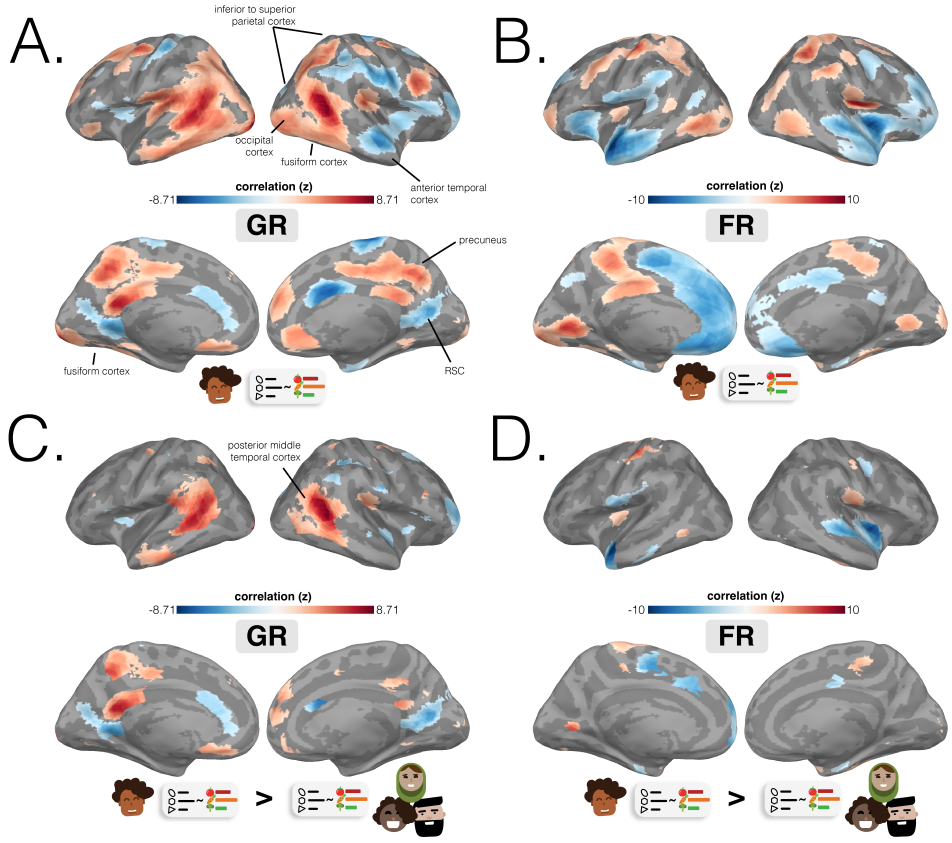

Figure 5–Figure supplement 1. Predicting POCN object reinstatement from room reliability. (A.) Regions where room reliability predicted POCN object reinstatement in guided recalls. **(B.)** Regions where room reliability predicted POCN object reinstatement in free recalls. **(C.)** Regions where room reliability predicted POCN object reinstatement in guided recalls and there was also a predictive benefit from participant-specific room reliability. **(D.)** Regions where room reliability predicted POCN object reinstatement in free recalls and there was also a predictive benefit from participant-specific room reliability. The surface maps presented in **A** and **B** were statistically thresholded by comparing correlations to a null distribution and then FDR-correcting for $q < 0.05$. The surface maps presented in **C** and **D** show the intersection of the participant-specific models (**A** and **B**) and the regions where there was a significant positive difference in the coefficient of determination between the original participant-specific model and the N-1 group model. Statistical significance for the differences between the coefficients of determination was determined by comparing the differences to a null distribution and FDR-correcting for $q < 0.05$. All four surface maps are colored based on the magnitude of the z-scored correlation values of the participant-specific model, with blue showing negative and red showing positive relationships, respectively.