Investigating the neural basis of schematic false memories by examining schematic and lure pattern similarity

By Catherine M. Carpenter & Nancy A. Dennis

The Pennsylvania State University

Corresponding Author:

Nancy Dennis, PhD.

nad12@psu.edu

The Pennsylvania State University

450 Moore Building

University Park, PA 16802

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Abstract

Schemas allow us to make assumptions about the world based upon previous experiences and aid in memory organization and retrieval. However, a reliance on schemas may also result in increased false memories to schematically related lures. Prior neuroimaging work has linked schematic processing in memory tasks to activity in prefrontal, visual, and temporal regions. Yet, it is unclear what type of processing in these regions underlies memory errors. The current study examined where schematic lures exhibit greater neural similarity to schematic targets, leading to this memory error, as compared to neural overlap with non-schematic lures, which, like schematic lures, are novel items at retrieval. Results showed that patterns of neural activity in ventromedial prefrontal cortex, medial frontal gyrus, middle temporal gyrus, hippocampus, and occipital cortices exhibited greater neural pattern similarity for schematic targets and schematic lures than between schematic lures and non-schematic lures. As such, results suggest that schematic membership, and not object history, may be more critical to the neural processes underlying memory retrieval in the context of a strong schema.

Introduction

Schemas provide us with a means for organizing the world around us and allow us to make inferences in new environments based upon previous experiences. In doing so, schemas aid in how we organize, encode, and retrieve information across a multitude of experiences. While schemas generally provide a large benefit to memory, schemas may also result in increased rates of false memories, particularly when novel information matches the schema (Lampinen et al., 2001). In fact, it is relatively common to find comparable true and false memory rates for schematic information over and above that of novel information (Lampinen et al., 2000; Miller & Gazzaniga, 1998; Neuschatz et al., 2002; Webb et al., 2016). This is interesting given that in visual memory paradigms assessing schematic memory, the schematic targets have been presented and studied whereas the schematic lures are novel objects with no perceptual overlap with the targets. In this sense, schematic lures are similar to non-schematic lures which have much lower false memory rates (Lampinen et al., 2000; Miller & Gazzaniga, 1998; Neuschatz et al., 2002; Webb et al., 2016; Webb & Dennis, 2020). While there has been extensive behavioral and quantitative univariate neural work in the realm of schematic false memory (Brewer & Treyens, 1981; Charlton & Leov, 2021; Kleider et al., 2008; Lampinen et al., 2001; Neuschatz et al., 2002; Webb & Dennis, 2020), the underlying neural mechanisms that promote schema-related increases in false memories to these visually distinct objects are less understood. Given the schematic relationship but visual distinction between schematic targets and lures in a visual memory study, we investigated whether the neural mechanisms underlying schematic lures resemble that of target items that share an overlapping schematic theme or whether they reflect that of novel, unique visual objects.

Behavioral evidence is largely conclusive that when schemas are used to support memory, schema-consistent information is well remembered (Alba & Hasher, 1983; Castel, 2005; Spalding et al., 2015; van Kesteren et al., 2012). Schemas act as a guide for integrating new memories and knowledge with prior experiences to form a holistic representation of an experience (Alba & Hasher, 1983). As such, schemas provide a scaffold and support for memory retrieval (van Kesteren et al., 2012). At the same time, these processes lead to schematic information not presented in the studied environment to also be erroneously endorsed as "old" in subsequent memory tests due to the overlap in the gist of prior experiences (e.g., Brewer & Treyens, 1981; Charlton & Leov, 2021; Kleider et al., 2008; Lampinen et al., 2001; Neuschatz et al., 2002; Webb & Dennis, 2020). For example, in the famous "room schema" study by Lampinen and colleagues (2001), participants exhibit higher false recall for schematically-related items found in an office (e.g., books) compared to atypical office items (e.g., mirror). The occurrence of high false memories rates has since been shown in numerous studies using both recall and recognition testing procedures (Charlton & Leov, 2021; Kleider et al., 2008; Lew & Howe, 2017; Neuschatz et al., 2002). Yet false memory rates amongst schematic images often fall below that of semantically related words (Coane et al., 2021; Dennis et al., 2015; Oliver et al., 2016). This may be related to the unique physical properties of schematic lure objects compared to their studied counterparts. In this study we ask what neural processing leads to lures being erroneously endorsed as "old" opposed to correctly being identified as novel objects during memory retrieval.

The fact that schematic lures are unique objects that, despite their conceptual link to materials studied, share no perceptual overlap with studied objects presents a unique question for how these objects are represented in memory. On one hand, schematic lures are highly related to

the studied material. For example, a sink is highly related to the concept of bathroom and is conceptually related to other objects in a bathroom schema such as toilet, shower, bathtub, and plunger. Yet schematic lures are also physically distinct from these objects, sharing no physical characteristics with them. Any false alarms to schematically related lures are therefore likely based upon that conceptual relationship, whereas perceptual features likely help to distinguish the object as a novel item during a memory test. Thus, from a neural perspective, this should create a dissociation in neural representations where schematic lures might resemble targets in regions processing schematic information, but not in regions that process visual details of objects in memory tasks.

Past neuroimaging work examining univariate activity has identified a role of several regions, including the ventromedial prefrontal cortex (vmPFC) and middle temporal gyrus (MTG), in supporting true schematic memories (Gilboa & Marlatte, 2017; van Kesteren et al., 2012, 2013; Webb et al., 2016). With respect to the vmPFC, this work posits that while encoding of novel information is initially medial temporal lobe (MTL) dependent, reactivation of schemas will result in a dependency on prefrontal cortices, with consistent schema-related activation occurring in the vmPFC (Brod et al., 2017; Gilboa & Marlatte, 2017; van Kesteren et al., 2010, 2012, 2013). Thus, we may utilize the vmPFC in addition to MTL regions to consolidate and process schema-consistent information if a prior schema exists (van Kesteren et al., 2012; Zeithamova et al., 2012). Specifically, researchers find that having a prior schema facilitates processing in the vmPFC and that increased coupling between the hippocampus (HC) and vmPFC is related to better memory performance for schematic information (van Kesteren et al., 2010). Interestingly, individuals with damage to the vmPFC exhibit a reduced reliance on schema-based processing (Spalding et al., 2015), as well as a reduction in schema-related false

memories (Warren et al., 2014). In addition to the supporting role of the vmPFC in true schematic memories, this work highlights a potential role of the vmPFC in promoting false memories to schema-consistent information. Accordingly, a nearby region, the medial prefrontal cortex (mPFC), which contains the middle frontal gyrus (MFG), has also been implicated in many studies of false memories, including schematic, perceptual, and semantically related false alarms (e.g., Abe et al., 2008; Dennis & Turney, 2018; Garoff-Eaton et al., 2007; for a meta-analysis see Kurkela & Dennis, 2016; Slotnick & Schacter, 2006; Turney & Dennis, 2017; Webb & Dennis, 2019). Taken together, results suggest that the schema-related activity in the mPFC may be a key component to the encoding and endorsement of false memories, particularly when the lure information is schematically or thematically related to studied information.

The middle temporal gyrus (MTG) is another region identified in numerous false memory studies, including those associated with semantic, schematic, and perceptual false memories (e.g., Dennis et al., 2007, 2008; Garoff-Eaton et al., 2006; Gilboa & Marlatte, 2017; Kubota et al., 2006; Slotnick & Schacter, 2006; Turney & Dennis, 2017; Webb et al., 2016; Webb & Dennis, 2019). In terms of studies examining schematic false memory, this region has been suggested to represent semantic gist related to the connection between the schema and the lure items (Webb et al., 2016; Webb & Dennis, 2019). Specifically, prior work finds that activation in the MTG is associated with both true and false schematic memories, including highly confident recollection-related memory errors and increasing in activation with regard to individual differences in false memory rates (Dennis & Turney, 2018; Webb et al., 2016). This work highlights the involvement of the MTG in semantic processing and how it may lead to the erroneous endorsement of lures based upon evaluating congruent information that is consistent with prior schemas. The above regions are clearly active when one makes an erroneous “old”

endorsement to a lure, however, it is unclear whether the underlying neural processing truly reflects that of target items.

While the foregoing regions have been found to process schematic properties of objects in a memory task, the visual cortex is known for its ability to discriminate between old and new information (Bowman & Dennis, 2015b; Kurkela & Dennis, 2016; Slotnick & Schacter, 2006). Specifically, the visual cortices exhibit unique patterns of neural activation during both perceptual processing (Haxby et al., 2001) and memory retrieval (Bowman & Dennis, 2015a, 2015b; Slotnick & Schacter, 2004, 2006; Stark et al., 2010; Vaidya et al., 2002; Webb et al., 2016; Wheeler et al., 2000) when objects are physically distinct from one another. Regarding false memory, while the visual cortex has shown greater similarity in processing perceptually related information (Bowman & Dennis, 2015a; Gutchess & Schacter, 2012), it has also been implicated in the correct rejection of lures that are more visually distinct from that presented during encoding (Bowman & Dennis, 2015a, 2015b). This suggests that the visual cortex is sensitive to different types of novelty processing and may support successful memory discrimination for semantically related, but perceptually novel, information (Bowman & Dennis, 2015a). Schematically related information should fall in this domain, being physically and perceptually unique in its composition compared to related items from the encoded schema. With regards to the visual cortex's role in both successful retrieval of schematic information and correct rejection of novel and related items, it is worthwhile to consider the underlying quality of relationships in visual regions with regards to how they process schematically related and novel information, and how that may relate to memory success or failure.

The current work aims to elucidate how schematic lures are represented neurally, specifically examining the similarity of neural patterns with that of both schematic target and

novel lures. While prior work has developed a greater understanding of the quantitative relationships of blood-oxygen-level-dependent (BOLD) activation associated with schematic processing, the qualitative relationships underlying those patterns has remained an open question. The purpose of our investigation is to examine the quality of these relationships using pattern similarity analyses to determine whether—and where, neurally—schematic lures are represented more similar to that of studied, schematic information or more similar to other unstudied novel information. In addition to elucidating the neural representations of schematic information, we are interested in examining whether these patterns correlate with false alarm rates. In the context of the current set of analyses we define schema as a cognitive framework that help us to organize, interpret, and synthesize information. With respect to the current design, we further operationalize a schema as a scene depicting a singular concept such as 'bathroom' or 'farm'. Included in the scene are objects that are best characterized by their membership in the schema. For example, a toilet is (typically) found in no other schema but that of bathroom (see Methods and Appendix A for additional details on schema inclusion).

We hypothesize that schematic information will have more similar neural patterns to one another irrespective of whether it was a target or lure trial at retrieval (e.g., object history), when compared to novel information (i.e., schematic and novel lures), and that this similarity will appear in the vmPFC, HC, and MTG regions. Yet we predict the opposite relationship in visual cortices, such that novelty irrespective of schematic association (e.g., both schematic and non-schematic lures) will show more similarity of neural patterns within the visual cortex, and in particular the early visual cortex which has been shown to be responsible for novelty and visual processing (Bowman & Dennis, 2015a; Kafkas & Montaldi, 2014; Koutstaal et al., 2001; Kurkela & Dennis, 2016; Slotnick & Schacter, 2006). This pattern of results would suggest that

there is greater neural confusability (Simmonite & Polk, 2022) between schematic information in regions that process schema information, but that novel signals are more prominent in regions that process the perceptual properties of the novel items. Finally, relating neural similarity to behavior, we hypothesize that this similarity between schematic information (irrespective of object history) is what drives high hit and false alarm rates to schematic lures. Considering that previous work finds similar rates between hits and false alarms of schematic information (Lampinen et al., 2001; Miller & Gazzaniga, 1998; Webb et al., 2016), we propose that this neural similarity may account for these behavioral similarities.

Materials & Methods

Participants: Fifty-five right-handed native English speakers from the Penn State University and State College community completed this experiment as a part of a primary analysis of comparing younger and older adults, however due to the lack of age differences in the behavioral results, the current set of analyses collapses across both (see results for these statistics). Four participants were excluded from the analysis due to head motion in excess of 4 mm. Two were excluded for excessive atrophy. Seven additional participants were also excluded for poor behavioral performance (greater than 50% miss rate for schematic targets; three for a no response rate greater than 30%), leaving data from 42 participants reported in all analyses [29 females; mean age= 47.5 years (SD=26.65)]. A post hoc power analysis was run at the request of a reviewer, which suggested a power analysis of 42 participants was sufficient to reach a medium effect size (Cohen's D= 0.5) and power of 89% using a one-sample t-test.

All participants provided written informed consent and received financial compensation for their participation. All experimental procedures were approved by The Pennsylvania State University's Institutional Review Board for the ethical treatment of human participants.

Stimuli and Task Procedure. The following information can also be found in Webb & Dennis (2016). Stimuli consisted of 26 schematic scenes (e.g., Bathroom, Farm), comprised of objects commonly associated with each schema (schematic targets: e.g., Farm: pig; Bathroom: toilet) as well as items unrelated to the schema (non-schematic targets: e.g., Farm: bush; Bathroom: vase). Lures consisted of both items commonly associated with each schema (schematic lures: e.g., Farm: tractor; Bathroom: sink), as well as non-schematic lures (e.g., piano, car, etc.) (See Fig 1.). All backgrounds and images were obtained from an internet image search. All items included in testing were normed for their association with each scene (See Webb and colleagues, 2016 for additional information). Each scene had an associated 4 schematic targets and 2-3 non-schematic targets at encoding. At retrieval, these 4 schematic targets, 2-3 non-schematic targets, 4 schematic lures were presented per scene in addition to 30 total non-schematic lures. (See Appendix A for full list of stimuli).

Encoding took place outside of the scanner while retrieval occurred in the scanner with approximately 30 minutes separating the two memory phases. Participants were asked to look at each scene and try to remember as much as they could for a later memory task. The 26 encoding scenes were presented for 10 seconds each across 2 runs, with 13 scenes presented in each run. During retrieval, all images (schematic targets from the scenes, schematic lures and non-schematic targets and lures) were presented in the center of the screen with three response options Remember, Know, New (RKN) displayed below each image. Participants completed 6 runs of approximately 7 minutes each in length at retrieval. Each image was displayed for 3 seconds. The images were pseudo-randomly sorted, ensuring that no more than 3 images from any one trial type appeared in a row and no 2 images associated with a given scene appeared in a row. In accordance with typical RKN task instructions, participants were told to respond

‘Remember’ if they could recollect specific details about the object such as its shape, color, placement in the scene or their thoughts or feelings during its initial presentation. Participants were told to respond ‘Know’ if the picture looked familiar, but they could not recollect any specific details of its prior presentation. They were told to respond ‘New’ if they believed the picture was not presented during the encoding session (see Figure 1). In total, there were 104 schematic targets, 104 schematic lures, 62 non-schematic targets and 30 non-schematic lures.

Images were projected onto a screen that participants viewed through a mirror attached to the head coil. Behavioral responses were recorded with the participant's right hand on a 4-button response box. Images were displayed by COGENT in MATLAB (Mathworks Inc., Natick, MA, USA). Noise in the scanner was reduced with headphones, and cushioning was provided in the head coil to minimize head motion.

Scanning parameters: Structural and functional images were acquired using a Siemens 3T scanner equipped with a 12-channel head coil, parallel to the AC–PC plane. Structural images were acquired with a 1,650 ms TR, 2.03 ms TE, 256 mm field of view (FOV), 256^2 matrix, 160 axial slices, and 1.0 mm slice thickness for each participant. Echo-planar functional images were acquired using a descending acquisition, 2,500 ms TR, 25 ms TE, 240 mm FOV, an 80^2 matrix, 90° flip angle, 42 axial slices with 3.0 mm slice thickness resulting in 3.0 mm isotropic voxels.

MRI Data Preprocessing: Results included in this manuscript come from preprocessing performed using fMRIPrep 20.1.1 (Esteban et al., 2019) which is based on Nipype 1.5.0 (Gorgolewski et al., 2011).

Anatomical data preprocessing: A total of 1 T1-weighted (T1w) images were found within the input BIDS dataset. The T1-weighted (T1w) image was corrected for intensity non-uniformity

(INU) with N4BiasFieldCorrection (Tustison et al., 2010), distributed with ANTs 2.2.0 (Avants et al., 2008), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid, white-matter and gray-matter was performed on the brain-extracted T1w using fast (FSL 5.0.9, Zhang et al., 2001). Brain surfaces were reconstructed using recon-all (FreeSurfer 6.0.1, 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 one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with antsRegistration (ANTs 2.2.0), using brain-extracted versions of both T1w reference and the T1w template. The following template was selected for spatial normalization: ICBM 152 Nonlinear Asymmetrical template version 2009c (Fonov et al., 2009; TemplateFlow ID: MNI152NLin2009cAsym).

Functional data preprocessing: For each of the 6 BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 5.0.9, Jenkinson et al., 2002). Susceptibility distortion correction (SDC) was omitted. The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer) which implements boundary-based registration (Greve & Fischl, 2009). Co-registration was configured with six degrees of freedom. The BOLD time-series (including slice-

timing correction when applied) were resampled onto their original, native space by applying the transforms to correct for head-motion. These resampled BOLD time-series will be referred to as preprocessed BOLD in original space, or just preprocessed BOLD. The BOLD time-series were resampled into standard space, generating a preprocessed BOLD run in MNI152NLin2009cAsym space. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (Satterthwaite et al., 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using antsApplyTransforms (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels (Lanczos, 1964). Non-gridded (surface) resamplings were performed using mri_vol2surf (FreeSurfer). Many internal operations of fMRIPrep use Nilearn 0.6.2 (Abraham et al., 2014), mostly within the functional processing workflow. For more details of the pipeline, see the section corresponding to workflows in *fMRIPrep*'s documentation.

Analyses: This study was pre-registered as a secondary analysis on a pre-existing data set on OSF: https://osf.io/mtd8r. This data has been published prior in a sample of younger adults (Webb et al., 2016) and in a sample of older adults (Webb & Dennis, 2019) examining univariate activation for schematic true and false memory.

Behavioral Analyses: At the request of a reviewer and for transparency purposes, four mixed model ANOVAs were run (Age: young or old, condition: schematic or non-schematic images) predicting both recollected and adjusted familiarity hits and false alarm rates. Adjusted familiarity hits were calculated as pKnow Hits/(1 - pRemember Hits) and adjusted familiarity FA were calculated as pKnow FA/(1 - pRemember FA). These calculations take into account the fact the recollection and familiarity are not mutually exclusive processes (Duarte et al., 2006, 2010; Yonelinas, 2002; Yonelinas & Jacoby, 1995). Main effects and interactions were parsed out using paired t-tests. These were conducted using the rstatix package in R Studio (Kassambara, 2021).

Pattern Similarity Analysis: To estimate neural activity associated with individual trials, separate GLMs were estimated in SPM12 defining one regressor for each trial at retrieval (Mumford et al., 2012). An additional six nuisance regressors were included in each run corresponding to motion. Whole-brain beta parameter maps were generated for each trial at retrieval for each participant. For any given parameter map, the value of each voxel represents the regression coefficient for that trial's regressor in a multiple regression containing all other trials in the run and the motion parameters. These beta parameter maps were next concatenated across runs.

The main regions of interest include the hippocampus (HC), the middle occipital cortex (MOC), inferior occipital cortex (IOC), middle frontal gyrus (MFG), middle temporal gyrus (MTG) (Webb et al., 2016; Webb & Dennis, 2019) and the ventromedial prefrontal cortex (vmPFC ; van Kesteren et al., 2010; Warren et al., 2014). Activation in HC and vmPFC has been associated with schema-consistent information (Guo & Yang, 2020; van Kesteren et al., 2010; Warren et al., 2014). Additionally, visual cortex, including the IOC and MOC, is known for its ability to discriminate between old and new information (Bowman & Dennis, 2015b; Kurkela &

Dennis, 2016; Slotnick & Schacter, 2006). Finally, activation in the MTG has been associated with false memories while the MFG has been implicated in both true and false memory (Webb et al., 2016). The ROIs were defined using anatomical masks of each bilateral region using the Wake Forest aal pickatlas in SPM12.

Two representational similarity analyses (RSA) were conducted to examine the overlap in representation of 1) schematic targets and schematic lures and 2) schematic lures and non-schematic lures at retrieval. Our analyses were aimed at identifying how object history (novel lure information) versus schematic membership (belonging to a schema) was represented neurally. The purpose of the RSA across schematic lures and non-schematic lure analysis was to identify regions that represented objective novelty across the two stimulus types (irrespective of schematic membership). Specifically, we aimed to explore to what extent neural patterns associated with schematic lures and non-schematic lures overlap. Additionally, the purpose of the RSA across schematic lures and schematic targets was to identify regions that represented schematic processing (irrespective of object history). Specifically, we aimed to explore to what extent neural patterns associated with schematic lures and schematic targets overlap.

Pattern analyses were conducted using the CoSMoMVPA toolbox (Oosterhof et al., 2016). Specifically, given our interest in understanding whether neural patterns seen with schematic lures are more similar to schematic target or non-schematic lure information, we compared the between-category similarity of lure information and schematic information irrespective of behavior. Additionally, we examined the between-category similarity of schematic hits and schematic false alarms to determine if increased pattern similarity is related to increases in false memories for schematic information. The similarities were directly tested via a paired t-test in RStudio. The similarity of schematic targets and lures will be referred to as

similarity between schematic information. The similarity of schematic lures and non-schematic lures will be referred to as similarity between lure information. Significant results were confirmed via 10,000 permutation t-tests using the Mkinfer package in R (Kohl, 2022). Following this initial analysis interested in trials at the condition level, we did not have enough trial numbers of false alarms to non-related lures to behaviorally bin trials in the "lure similarity" analysis (see results for reporting of averages). This was a secondary data analysis, and the initial purpose of the study was not to examine non-schematic lures but rather focused on schematic targets and lures. Thus, the original design had fewer trial types in the design of the task.

Exploratory RSA Searchlight: To investigate neural similarity in regions outside of our a priori ROIs, we executed the foregoing analysis using a whole brain mask of the cortex as an exploratory analysis. These analyses were conducted using the representational similarity analysis searchlight implemented in CoSMoMVPA toolbox (Oosterhof et al., 2016). Both analyses used a searchlight radius of 6 mm. The beta maps were then submitted to a paired t-test using SPM12 (http://fil.ion.ucl.ac.uk/spm/) to examine where similarity was greater for schematic information compared to lure information and vice versa. Due to the exploratory nature of this analysis, all second level results were thresholded at $p<.001$ using an extent threshold of 11 voxels based off AFNI's 3dClustSim (Cox, 1996; Cox & Hyde, 1997).

Results

Behavioral Results: A 2x2 (age: old, young; Condition: schematic, non-schematic) mixed model ANOVA predicting recollected hits revealed no main effect of age ($F(1,40) = 0.09$, $p=0.76$, pes=.002), nor interaction between condition and age ($F(1,40) =1.83$, $p=.18$, pes=.044). A main effect of condition was revealed, $F(1,40) = 253.36$, $p<.001$, pes=.86, such that there were greater

recollected hits to schematic targets (M=0.44, SD=0.13) compared to non-schematic targets (M=0.23, SD=0.12).

A 2x2 (age: old, young; Condition: schematic, non-schematic) mixed model ANOVA predicting adjusted familiarity hits revealed no main effect of age ($F(1,40) = 1.09$. $p = .30$, pes=.026), nor interaction between condition and age ($F(1,40) = 0.64$, $p = .43$, pes=.016). A main effect of condition was revealed, $F(1,40) = 6.28$, $p = .016$, pes=0.14, such that there were greater familiarity hits to schematic targets (M=0.46 SD=0.16) compared to non-schematic targets (M=0.42, SD=0.18).

A 2x2 (age: old, young; Condition: schematic, non-schematic) mixed model ANOVA predicting recollected FAs revealed that there was no main effect of age ($F(1,40) = 0.10$. $p = .75$, pes=.003), nor interaction between condition and age ($F(1,40) = 0.43$, $p = .52$, pes=.011). A main effect of condition was revealed, $F(1,40) = 94.82$, $p < .001$, pes=.70, such that there were greater recollected FAs to schematic lures (M=0.23, SD=0.14) compared to non-schematic lures (M=0.07, SD=0.07).

A 2x2 (age: old, young; Condition: schematic, non-schematic) mixed model ANOVA predicting adjusted familiarity FAs revealed that there was no main effect of age ($F(1,40) = 0.12$, $p = .73$, pes=.003), nor interaction between condition and age ($F(1,40) = 0.005$, $p = .94$, pes=.0001). A main effect of condition was revealed, $F(1,40) = 106.23$, $p < .001$, pes=.72, such that there were greater adjusted familiarity FAs to schematic lures (M=0.41, SD=0.15) compared to non-schematic lures (M=0.20, SD=0.17).

As there were no main effects or interactions with age behaviorally, all neural analyses were collapsed across age.

Pattern Similarity Results: Two RSAs were run and compared via a t-test. Schematic information refers to the RSA between schematic targets and schematic lures, while lure information refers to the RSA between schematic lures and non-schematic lures. There was significantly greater similarity between schematic information than lure information in the vmPFC, the MOC, and in the IOC, [$t(41) = -2.40$, $p=0.021$; $t(41) = -5.21$, $p<.001$; $t(41) = -3.94$, $p<.001$ respectively]. There were no significant differences between the neural similarity of schematic information and lure information in the MTG, MFG or HC (all p's>.05) (see Table 1 for means). The current pattern of results indicates that overlapping neural patterns of schematic information, in the early and late visual cortices as well as the vmPFC, irrespective of whether subjects had seen it before or not, is more similar than information that is completely novel (see Figure 2 for RSA visualization).

Exploratory RSA Searchlight: A contrast for similarity between lure information greater than similarity between schematic information (schematic lure & non-schematic lure similarity > schematic target & schematic lure similarity) of two searchlights conducted within a whole brain mask revealed no significant clusters. Additionally, a contrast for similarity between schematic information greater than similarity between lure information (schematic target & schematic lure similarity > schematic lure & non-schematic lure similarity) of two searchlights conducted within a whole brain mask revealed several significant clusters in the superior frontal gyrus and superior medial gyrus, HC, MFG and in the MTG (see Table 2 for full results and voxel locations and Figure 3 for visualization).

Pattern Similarity and Behavior: Since the above pattern similarity analyses were conducted on only target and lure information, we also wanted to directly determine whether neural pattern similarity between schematic hits and schematic false alarms was associated with increased hits

and false alarms as well. Due to low false alarm numbers (avg = 1.98 FAs) in the non-schematic lure condition, we were unable to correlate or perform a powerful enough representational similarity analysis with behavior associated with this condition. Thus, we conducted an RSA to examine the neural similarity between recollected schematic hits and schematic false alarms to directly correlate to behavior. There were no significant correlations between pattern similarity for schematic recollected hits and schematic recollected false alarms with recollected hits or recollected false alarms (all p's>.05).

Discussion

The current study aimed to determine the neural mechanisms underlying false memories to schematic lures specifically in relation to schematic targets and non-schematic lures. In line with our predictions, several brain regions implicated in schematic processing, including the vmPFC and bilateral MTG, exhibited greater neural similarity regarding schematic content, irrespective of object history (i.e., schematic targets and schematic lures), as opposed to object novelty (i.e., schematic lures and unrelated lures). Contrary to our predictions, the same pattern of results was also observed throughout visual cortices, including both early and late visual cortices. In fact, no brain region demonstrated greater similarity in neural processing with respect to object novelty. This suggests that a relationship with previous schematic knowledge is more influential when processing novel information than object history itself. The results highlight the critical relationship between information belonging to a common schema and underscore how related information is processed in a manner that leads to its misidentification in memory tasks.

Greater neural pattern similarity for schematic targets and schematically related lures compared to that of both types of lures within the vmPFC and bilateral MTG is consistent with a larger literature implicating these regions in schematic processing. Specifically, the finding that

the vmPFC exhibits greater neural similarity between schematic information expands upon prior work examining schemas at a univariate level (Guo & Yang, 2020; van Kesteren et al., 2010, 2013; Webb et al., 2016; Webb & Dennis, 2019) by informing us about the nature of the relationships between neural patterns in this region. Specifically, prior work has shown that the vmPFC is active during both the encoding and retrieval of schematic information (van Kesteren et al., 2010, 2013). The current work extends these findings suggesting that the schematic processing at retrieval underscoring targets is similar to that of schematic lures in this region, highlighting the broad nature of schema processing within the vmPFC. Given that there is greater neural similarity, and thus greater neural confusability, within this region for schematic information compared to novel information (Simmonite & Polk, 2022), this may also point to a common neural mechanism underlying high rates of both false alarms and hits to schematic information. However, as we did not find any correlations to behavior, future work is needed to confirm this relationship between pattern similarity and behavior.

While the MTG, MFG, and MTL ROIs as a whole did not exhibit significant differences in pattern similarity across trial types, an exploratory RSA searchlight identified greater neural similarity patterns for schematic information compared to lure information in clusters of voxels in all three regions. Specifically, greater schematic processing was found in the left and right MTG. This indicates that while ROI as a whole is not sensitive to differences across stimulus categories, specific components within the MTG represent schematic information more similarly than novel information. In addition to a similar pattern found in the vmPFC, results suggest that subcomponents of these regions process schematic information in a similar manner irrespective of the item's history. With respect to the MTG, this finding also extends prior univariate work showing that the MTG is active during false memories, as well as work showing that activity in

this region increases with respect to false memory rate (Dennis et al., 2007, 2008; Garoff-Eaton et al., 2006; Gilboa & Marlatte, 2017; Kubota et al., 2006; Slotnick & Schacter, 2006; Turney & Dennis, 2017; Webb et al., 2016; Webb & Dennis, 2019). The current findings suggest that similarity in schematic processing, including schematic gist related to lure information, underlies these past findings. Taken together, the findings across vmPFC and MTG support our hypotheses regarding greater pattern similarity in regions responsible for processing schematic information irrespective of item history.

The searchlight analysis also identified a large cluster of voxels within the right MFG, left posterior HC, and left anterior parahippocampal gyrus (PHG) as showing greater neural pattern similarity across schematic targets and schematic lures compared to both types of lures. Similar to the vmPFC and MTG, the MFG has been implicated in semantic processing (Binder et al., 2009; Kircher et al., 2001; Mummery et al., 2000; Noppeney & Price, 2002; Wise & Price, 2006) and the retrieval of semantic gist (Buckner & Petersen, 1996; Gabrieli et al., 1998; Mummery et al., 2000; Noppeney et al., 2007; Simons et al., 2005; Wise & Price, 2006). While these regions did not show significant similarity between schematic targets and schematic lures in the ROI similarity analysis, their presence in the whole brain searchlight analysis indicates that subcomponents of these regions are indeed more sensitive to schematic properties of stimuli compared to object novelty. These findings highlight the importance of taking into account both laterality and more focal regions when examining fine-grained differences in neural similarity related to memory processing. Specifically, subregions of the HC and MFG may be more influential in representing patterns of similarity compared to the region at large. Greater similarity across schematic stimuli, opposed to novelty, continues to highlight the ubiquitous nature of semantics in memory processing, with semantic and schematic information biasing the

way novel stimuli not previously studied during encoding is processed at the time of retrieval. Interestingly, this bias also extends to retrieval-related representations within the MTL. The HC and PHG, are typically seen in the literature as being responsible for the retrieval of previously encoded memory traces. In the case of target items, this would include representing the schematic relationship associated with objects. Yet, for lures, while the objects encompass the same schematic gist, there is no encoded trace to be retrieved. Common processing across targets and lures in the MTL may represent retrieval of this shared schematic gist incorrectly bound to the representation of the lure object. This error in neural processing within the MTL may be a critical factor in the lure item being incorrectly identified as "old", leading to the high rate of false memories in schematic-based memory paradigms.

While overlapping schematic representations and gist processing was expected for targets and lures that are related to the encoding schema within regions previously implicated in schematic processing, it was expected that neural patterns in visual cortices would exhibit a dissociation between the two trial types. Specifically, given the absence of perceptual overlap between schematic lures and schematic targets, we expected visual processing regions to represent all novel information more similarly than the schematic information. Returning to the example in the introduction of the bathroom sink, this sink lure shares no perceptual features that are seen in target items from the encoded schema, such as a toilet or bathtub. This novelty of item identity and perceptual properties should be beneficial to memory processing and elicit unique processing within the visual cortices that would allow for the objects' correct rejection in memory testing (Bowman & Dennis, 2015a, 2015b). However, both the IOC and MOC ROIs showed greater pattern similarity for schematic information irrespective of object history: the same pattern as observed in the vmPFC and MTG.

Prior univariate analyses conducted on this data found that visual regions were capable of distinguishing between true and false recollection of schematic information (Webb et al., 2016). However, the current pattern similarity analyses suggest that, despite this difference, neural patterns in visual cortices are more closely related for objects (irrespective of whether it was a target or lure) that share a common schema than for objects sharing a common presentation history. While contrary to our predictions, this is interesting regarding the often observed high false alarm rate in schematic memory studies. Results suggest that not only is a schema signal coming from regions such as vmPFC and MTG, which are known for processing relatedness amongst schematic items (van Kesteren et al., 2010, 2013; Webb et al., 2016; Webb & Dennis, 2019), but also from regions that are known for processing more discrete object properties such as the early and late visual cortices (Bowman & Dennis, 2015a; Gutchess & Schacter, 2012; Slotnick & Schacter, 2004, 2006). This level of similarity may also underlie greater confusability across targets and schematic lures, leading to both being identified as "old" at high rates during memory responses. That is, the neural patterns may be too similar across schematic targets and lures to correctly reject the related lure even though the lure is completely new and not part of the studied set. Previous work asserts that object history is critical to activation in visual regions, as well as critical to novelty detection (Bowman & Dennis, 2015a; Gutchess & Schacter, 2012; Slotnick & Schacter, 2004, 2006). However, the current results expand the nuance surrounding this idea, suggesting that information belonging to a prior schema may be more influential than object history with respect to processing in visual cortices (and throughout the brain), leading to its persuasive influence on memory processing over and above object novelty.

Finally, compared to neural pattern similarity for schematic information, lure similarity showed no significant clusters in the similarity searchlight. That is, no region, either within our

a-priori ROIs nor through our searchlight analysis, exhibited greater neural similarity for item novelty greater than schematic similarity. This indicates that there is widespread similarity across the brain for schematic information, which overrides object history in terms of pattern similarity. This again highlights the pervasive influence of schemas throughout the brain in regions apart from those hypothesized initially that is not the case for novel information. While not directly related to behavior, these results suggest a mechanism behind why false memories to schematic information are so prevalent compared to that of novel information. This also replicates our ROI-based pattern similarity analyses that suggest that there is enhanced similarity amongst schematic information and thus dissimilarity amongst lure information in comparison.

Interestingly, despite the neural similarity for schematic information within cortical and subcortical regions, neural processing leads to the identification of novel information even when there is overlap in schematic relationships and neural signals between targets and lures. Thus, despite this similarity, this confusability can be overridden to an extent to allow for successful memory performance. However, absent of any region showing greater pattern similarity for item novelty than schematic similarity, this suggests that while schematic similarity *can* be overcome during memory retrieval (e.g., correct rejections to schematic lures), this may be a particularly difficult process given the neural bias related to the processing of schematic content when viewing objects part of a known schematic category of stimuli. Combined with the fact that participants also exhibit higher hit rates to schematic targets compared to non-schematic targets (Lampinen et al., 2001; Miller & Gazzaniga, 1998; Webb et al., 2016; Webb & Dennis, 2019), these findings support the prevalent nature of schemas in memory processing. However, absent of correlations with behavior, further work is needed to directly link schematic processing with memory performance across both successful and unsuccessful memory responses.

Taken together, the current results suggest that previous knowledge of a certain schematic event has a greater impact on neural processing than the novelty of information across multiple brain regions including prefrontal, MTL, and visual cortices. Specifically, these and many other brain regions represent schematic information across items more similarly than object history. Most interestingly, this similarity of processing was found not only within regions known for schema processing, but throughout the brain, including clusters of voxels within the MTL and occipital cortices which have been traditionally associated with memory success. This similarity in neural processing across targets and lures may be why people false alarm at higher rates to schematic lures compared to non-schematic lures; however, given our absence of brain-behavior correlations and low false alarm numbers regarding the non-schematic trials, this latter point would need further work to verify. Finally, no brain region exhibited higher neural pattern similarity as a function of item history, suggesting that schematic processing is a strong predictor of neural activity above and beyond object novelty.

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Declaration of Interest Statement

The authors report there are no competing interests to declare.

Data Availability Statement

Data may be made available upon request of the corresponding author.

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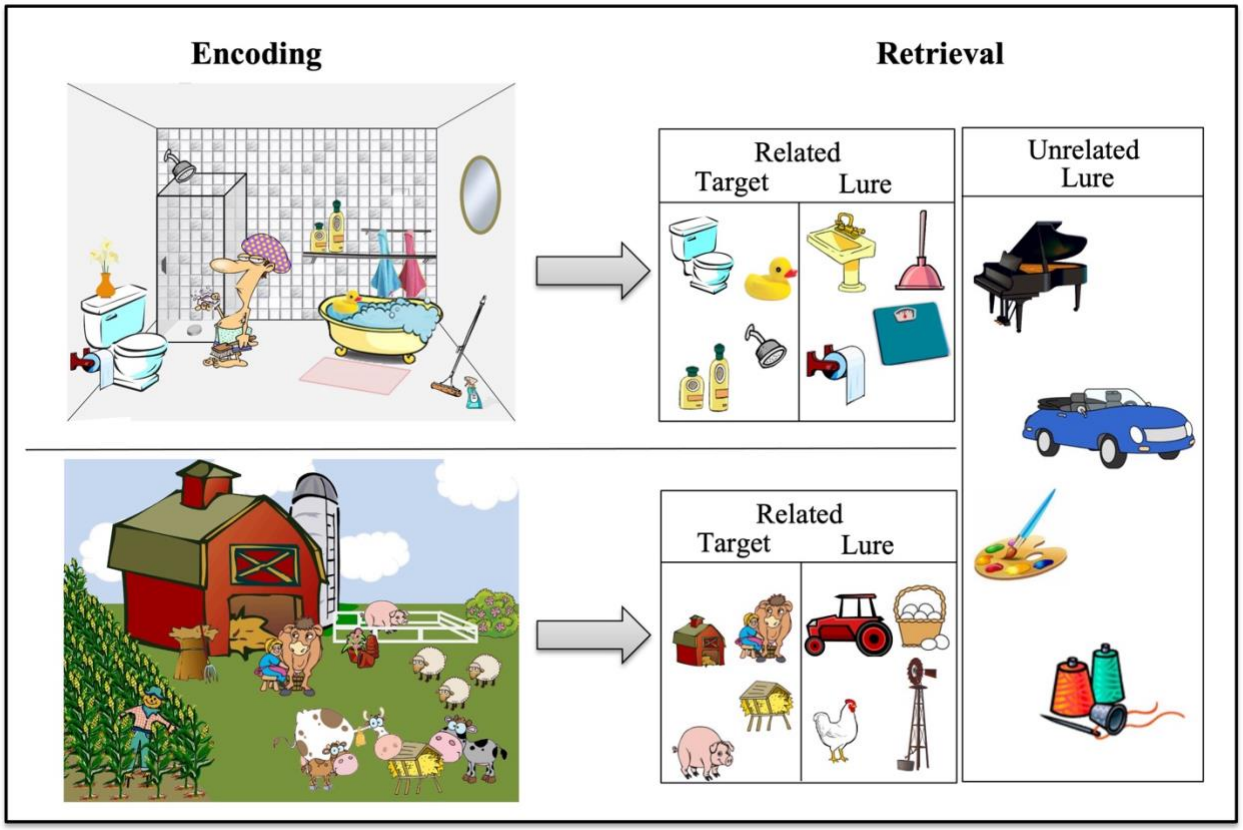

Figure 1. Task paradigm of two scenes seen at encoding and items seen at retrieval.

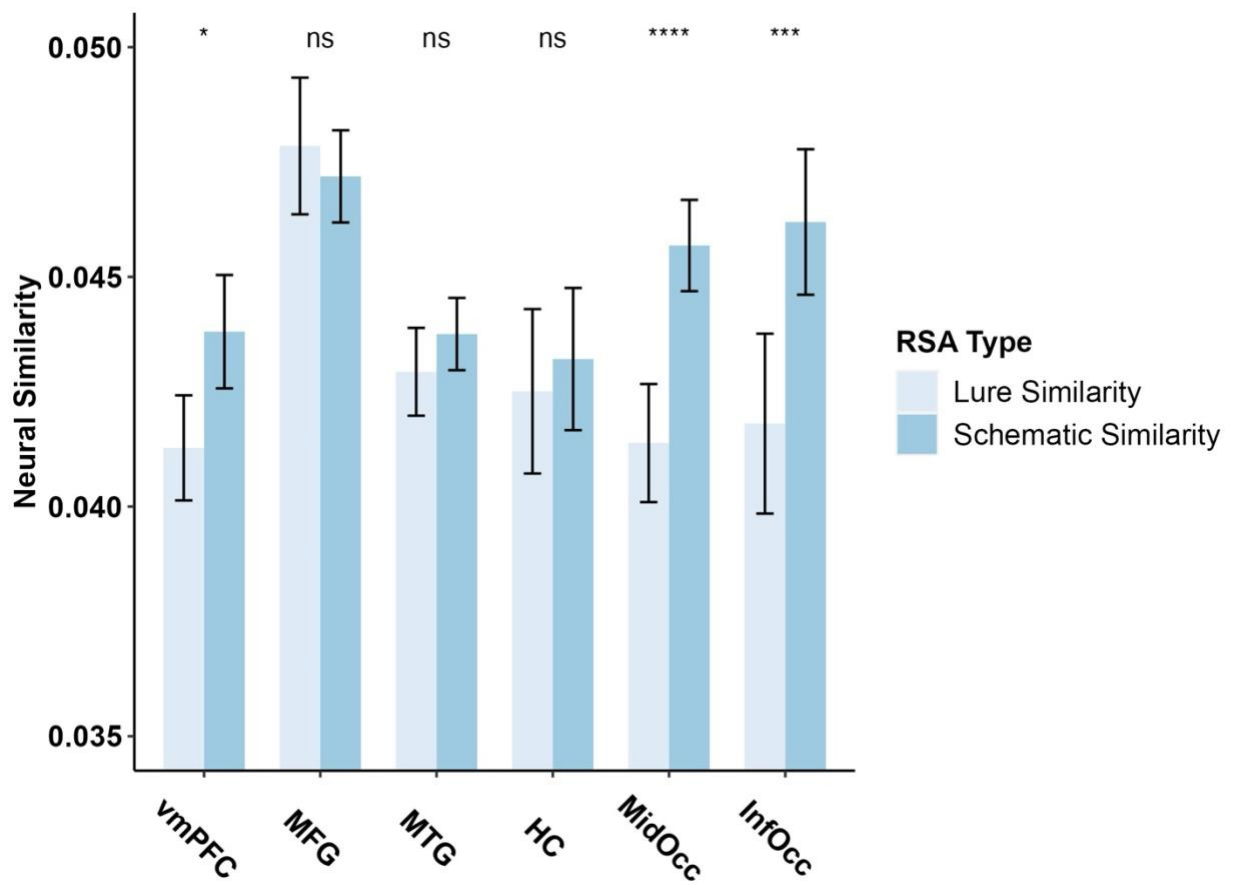

Figure 2. RSA Figure examining the difference between neural similarity of lures (novel lures and schematic lures) and schematic information (schematic targets and schematic lures). *Lure Similarity* = Similarity between Schematic Lures & Non-Schematic Lures; *Schematic Similarity*= Similarity between Schematic targets & Schematic Lures. ROI = region of interest.

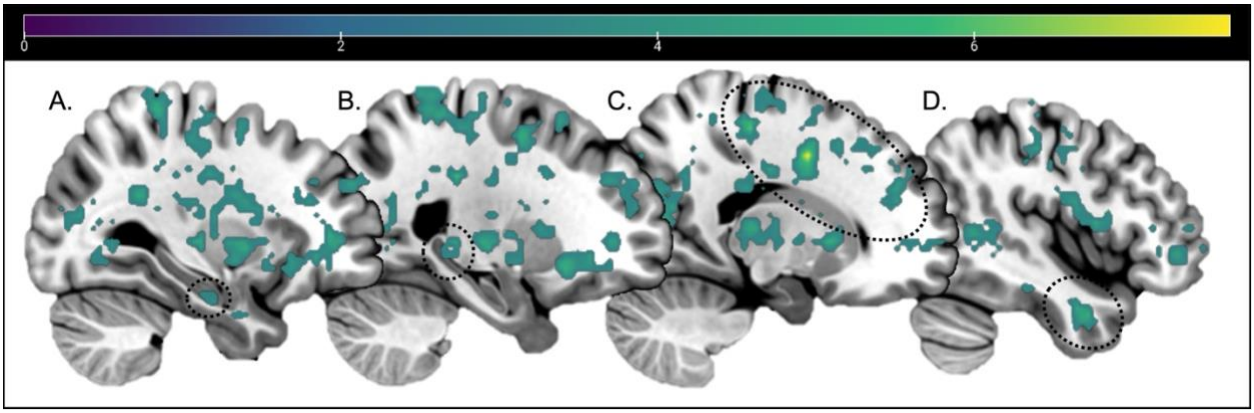

Figure 3. Whole Brain RSA searchlight contrast results for Schematic information similarity > Lure information similarity, thresholded at $p<.001$ and 11 voxels. No clusters survived thresholding for Lure information similarity > Schematic information similarity. Sagittal slices: -30, -24, 17, 44. Dotted circles around: [A] Anterior HC, [B] Posterior HC, [C] MFG, [D] MTG. Color bar indicates t-values.

	Schematic Similarity	Lure Similarity
	M(SD)	M(SD)
vmPFC*	0.044 (.01)	0.041 (.01)
MFG	0.047 (.01)	0.048 (.01)
MTG	0.044 (.01)	0.043 (.01)
HC	0.043 (.01)	0.043 (.01)
MOC****	0.046 (.01)	0.041 (.01)
IOC***	0.046 (.01)	0.042 (.01)

Table 1. Means and standard deviation of pattern similarity between schematic information (schematic targets and lures) and lure information (schematic and novel lures).

	BA	Hemisphere	k	t	x	y	z {mm}
Schema > Lure Similarity							
Superior-medial Frontal Gyrus	10	R	16	4.51	12	60	18
Ventral-medial Prefrontal Cortex	10	M	47	4.87	8	56	-4
	11	M	11	4.65	8	24	-18
Middle Frontal Gyrus	24	R	1477	8.58	18	2	42
Precentral Gyrus	44	R		6.85	50	6	8
	9	R	14	4.65	36	38	36
	6	R	16	4.05	18	6	56
Superior Frontal Gyrus	-	L	11	4.71	-30	32	20
Caudate	-	L	14	5.17	-12	12	0
Middle Temporal Gyrus	21	R	63	5.87	44	2	-30
	21	L	87	5.85	-60	-24	-6
Anterior PHG/Hippocampus	20	L	37	5.2	-40	-10	-30
Posterior Hippocampus	-	L	22	4.9	-24	-30	2
Cingulum	23	M	46	4.73	-4	-22	30
Thalamus	-	R	128	5.89	20	-24	8
Fusiform Gyrus	20	R	31	4.66	42	-28	-16
Paracentral Lobule	4	L	1856	6.31	-12	-34	72
Postcentral Gyrus	6	L		6.29	-54	-4	42
Putamen/Globus Pallidus	-	L		6.28	-22	-12	2
Cingulate	-	M	11	4.59	-4	-46	6
Precuneus	31	M	13	5.23	-6	-64	36
Occipital Gyrus	19	R	147	5.79	36	-54	2
	-	L	171	5.75	-34	-66	8
Middle Occipital Cortex	18	R	265	6.4	18	-84	0
Inferior Occipital Cortex	18	L	15	4.69	-24	-88	-4
Lure > Schema Similarity							
no significant clusters							

Table 2. RSA Searchlight results. PHG = parahippocampal gyrus; H= hemisphere; k = cluster threshold; t = statistical peak t-value; MNI x, y, and z coordinates; BA= Brodmann Area.

Appendix A.

	Schematic		Non-schematic
SCENE	**Targets**	**Lures**	**Targets**
AIRPORT	Car rental sign	Airline pilot	End table
	Departure gate sign	Gate sign	Restroom sign
	Man holding suitcases	Luggage rack	TV
	Man picking luggage	Security guard	
BATHROOM	Rubber duck	Bathroom floor scale	Flower vase
	Shampoo bottles	Sink	Mirror
	Shower head	Toilet paper roll	Spray bottle
	Toilet	Toilet plunger	
BEACH	Beach ball	Flip flops	Red wagon
	Beach umbrella	Sand pail/shovel	Sun
	Sandcastle	Snorkeling goggles	
	Surfboard	Suntan lotion bottle	
BIRTHDAY	Balloon	Birthday cake	Ice cream cone
	Birthday clown	Happy Birthday sign	Rug
	Birthday presents	Party hat	Scenic picture frame
	Piñata	Party noisemaker	
CAMPING	Campfire	Fishing pole	Folding chair
	Canoe	Food cooler	Lightening bug
	Lantern	Oar	Squirrel
	Tent	Sleeping bag roll	
CHRISTMAS	Christmas train	Candy cane	Cat
	Christmas tree	Christmas stocking	Family photo
	Holiday wreath	Mistletoe	
	Santa sleigh decoration	Nutcracker	
CHURCH	Altar	Bible	Flower arrangement
	Baptismal font	Jeweled chalice	Wooden stand
	Crucifix	Organ	
	Stained glass nativity	Rosary	
CINDERELLA	Cinderella & Prince Charming	Glass slipper	Lamp post
	Cinderella carriage	Magic horses	Topiary

	Clock tower	Mouse friend (Mary)	
	Fairy godmother	The Grand Duke	
CIRCUS	Circus elephant	Cannon stunt man	Light
	Ringleader	Circus juggler	Umbrella
	Ring of fire stunt	Seal balancing ball	
	Trapeze artist	Unicycling clown	
DOCTOR OFFICE	Blood pressure cuff	Doctor bag & stethoscope	Newspaper
	Examination table	IV bag	Rolling stool
	Medical tools	Nurse	
	Medicine rack	Physician scale	
FARM	Barn	Basket of eggs	Flower bush
	Cow being milked	Rooster	Flowerpots
	Hay bale	Tractor	
	Pig	Windmill	
FOOTBALL	Cheerleaders	Foam finger	Bench
	Coach	Football	Duffel bag
	Gatorade dispenser	Goal posts	
	Referee	Scoreboard	
FOURTH OF JULY	American flag	Eagle	Bicycle
	Kid playing baseball	Patriotic chef	Hamburger
	Patriotic themed pie	Sparkler	
	Small grill	Uncle Sam hat	
GOLF	Golf ball	Golf bag	Hot air balloon
	Golf cart sign	Golf cart	Rabbit
	Golfer	Hole information sign	Table & chairs set
	Hole flag	Tee	
GYM	Hand weights	Dumbbell holder	Coat rack
	Man exercising	Gym sneakers	Portable boombox
	Treadmill	Man doing yoga	Window
	Weightlifting duo	Weight bench	
HALLOWEEN	Black arched cat	Frankenstein	Moon
	Ghost	Jack-o-lantern	Paper bag
	Human skull	Witch's cauldron	

	Witch	Zombie	
KITCHEN	Coffee pot	Dishwasher	Pet bowls
	Microwave	Refrigerator	Wine bottle
	Oven mitt	Rolling pin	
	Stove	Toaster	
CHILD'S NURSERY	Alphabet blocks	Baby booties	Lamp
	Child playpen	Baby bottle	Laundry
	Rattle	Pram stroller	
	Teddy bear	Toy rocking horse	
OFFICE	Computer monitor	Briefcase	Tissue box
	Filing cabinet	Calculator	Trash can
	Memo pad	Desk phone	Wall clock
	Office worker	Mouse & mouse pad	
PARK	Kid catching frisbee	Ride-on horse rocker	Bird
	Park bench	Playground merry-go-round	Butterfly
	Playground jungle-gym	Slide	Kite
	Sandbox	Soccer ball	
POOL	Boy swimming	No running sign	First aid kit
	Diving board	Pool skimmer	Girl with ball
	Inner tube	Swimming sign	
	Life preserver	Towel	
SAFARI	Roaring lion	Binoculars	Tree
	Safari jeep	Bison skull	Well
	Wildlife photographer	Ostrich	
	Zebra	Rhinoceros	
SCHOOL/CLASSROOM	Alphabet sign	Composition notebook	Bookshelf
	Apple	Overhead projector	Recycling bin
	Child's backpack	School bell	Speaker
	Pencil sharpener & pencils	Scissors	
SKI SLOPE	Ski lodge	Gondola	Beaver
	Ski sign	Skier	Dog
	Snowboarder	Skis	Helicopter
	Snowman	Snowmobile	

THANKSGIVING	Cornucopia	Cooked turkey	Log
	Male pilgrim	Harvest food basket	Table
	Native American	Hunting rifle	
	Turkey	Pilgrim hat	
UNDERWATER	Octopus	Dolphin	Boot
	Puffer fish	Eel	Glass bottle
	Seahorse	Lobster	
	Treasure chest	Starfish	
UNRELATED LURES (NOT ASSOCIATED WITH ANY SCENE)	Astronaut, Bride and groom, Chessboard, Convertible, Cowboy boot, Cupid, Detour sign, Dump truck, Film reel, Flower bouquet, Game controller, Gavel, Grocery cart, Hammer, Handcuffs, High heels, Hockey player, Magnifying glass, Money, Nail polish bottle, Needle and thread, Paint palette, Piano, Pot of gold, Remote controller, Rocket ship, Saxophone, Sombrero, Sword, Test tubes		