Cognitive tasks affect the relationship between representational pattern similarity and subsequent item memory in the hippocampus

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ABSTRACT

Episodic memories are records of personally experienced events, coded neurally via the hippocampus and surrounding medial temporal lobe cortex. Information about the neural signal corresponding to a memory representation can be measured in fMRI data when the pattern across voxels is examined. Prior studies have found that similarity in the voxel patterns across repetition of a to-be-remembered stimulus predicts later memory retrieval, but the results are inconsistent across studies. The current study investigates the possibility that cognitive goals (defined here via the task instructions given to participants) during encoding affect the voxel pattern that will later support memory retrieval, and therefore that neural representations cannot be interpreted based on the stimulus alone. The behavioral results showed that exposure to variable cognitive tasks across repetition of events benefited subsequent memory retrieval. Voxel patterns in the hippocampus indicated a significant interaction between cognitive tasks (variable vs. consistent) and memory (remembered vs. forgotten) such that reduced voxel pattern similarity for repeated events with variable cognitive tasks, but not consistent cognitive tasks, supported later memory success. There was no significant interaction in neural pattern similarity between cognitive tasks and memory success in medial temporal cortices or lateral occipital cortex. Instead, higher similarity in voxel patterns in right medial temporal cortices was associated with later memory retrieval, regardless of cognitive task. In conclusion, we found that the relationship between pattern similarity across repeated encoding and memory success in the hippocampus (but not medial temporal lobe cortex) changes when the cognitive task during encoding does or does not vary across repetitions of the event.

Keywords: encoding variability; context variability; episodic memory; fMRI; representational similarity analysis; hippocampus

1.1 Introduction

Episodic memory provides long-term storage of personally experienced events. The information encoded in this memory system is learned in a single exposure and is linked to a context. That context can include time, space, and any other factors that change slowly or are continuous across many events, including cognitive factors (e.g., task instructions or goals). It is well-established that a functional medial temporal lobe (MTL)[1] memory system is necessary to encode new event memories (e.g., Corkin, 2002; Rosenbaum et al., 2005). Episodic memories are thought to result from biological coding via neuronal patterns of connection and communication. Functional magnetic resonance imaging (fMRI) can be used to study biological coding in the brain via the pattern of blood-oxygenated-level-dependent (BOLD) signal measured in individual voxels (approximately 3 mm^3). Although voxel patterns do not capture the precise, neuronal level, biological representation of a memory, a number of studies indicate that voxel patterns contain information about stimulus characteristics, categorization, novelty, and more (e.g., Dimsdale-Zucker et al., 2018). Importantly, voxel patterns can be used to predict whether an event will later be retrieved from memory (e.g., Karlsson Wirebring et al., 2015). The current study examines the relationships between voxel patterns for events that are repeated, in an effort to understand how similar events are coded in the MTL memory system and how cognitive factors affect those codes.

When a person encounters an object, perhaps lying at the side of a road, their brain creates a neural representation of that event, like those described above, that will be encoded into the MTL memory system, to allow later retrieval of that encounter. However, it is unlikely that

[1] Abbreviations: MTL, medial temporal lobe; fMRI, functional magnetic resonance imaging; BOLD, blood-oxygenated-level-dependent; RSA, representational similarity analysis; ITIs, intertrial intervals; PHc, parahippocampal cortex; PRc, perirhinal cortex; LSS, least squares separate model

the neural representation created will be the same for a person encountering the object in the context of their daily jogging routine as it would be for a person encountering the object in the context of supervising children who are playing in the adjoining yard. In instance one, encoding would likely be cursory and perhaps focused on navigation around the object or tripping risk. In instance two, encoding might be more effortful and focused on any perceived hazard to the children. If the neural representation of an object or an event differs due to the current cognitive state or goals, then the circumstances under which that object or event is likely to be retrieved will also differ. In other words, the encoded neural patterns that will best support later episodic retrieval may depend on cognitive goals during that encoding.

Existing studies of neural representations using multivoxel pattern analysis or representational similarity analysis (RSA) have not manipulated the cognitive state and surrounding context in order to determine how this might change the neural representation of an object or event. For example, participants in a prior study were asked to make judgments about a fixation cross while images were passively presented in the background (LaRocque et al., 2013). The neural patterns during that task were then sorted according to which of the passively presented images was later recognized or forgotten in a surprise memory test. Such results are often interpreted as indicating the universal characteristics of neural representations that support later memory retrieval. Yet, it is unknown whether the same results would be found if the participant were asked to ignore the fixation cross and instead provide the most specific verbal label possible for the image. Perhaps the relationship between representational similarity and later memory retrieval changes when events are effortfully dissociated as compared to when they are effortfully generalized (e.g., by categorizing the picture very broadly as a scene or object). This same idea was proposed in a recent review of RSA findings (Brunec et al., 2020), where it was clear that studies with a range of cognitive factors have produced variable conclusions about the relationship between representational similarity and memory. The authors of that review proposed that “situation-specific goals can shape neural responses” (Brunec et al., 2020, p. 204) and argued for more attention to stimulus characteristics, cognitive goals, and individual differences in the study of neural representations. The current project was designed to investigate how manipulating cognitive goals might affect RSA findings.

Another purpose of the current project is to investigate why contextual variability during encoding benefits later recognition of an item. Recent studies in our lab (Salan et al., under review) and in other labs (Sievers, Bird, et al., 2019) have investigated the effects of contextual variability and found that memory for an item is improved when the circumstances of encountering that item vary, as opposed to when they remain the same. Returning to the earlier example, if the same person encounters an object lying by the side of the road multiple times, we have found that their memory for the object will be stronger if it is encountered once while beginning their daily jog and a second time while supervising children in the yard than if it is encountered twice in either of the two scenarios. We have proposed several mechanisms that might explain the benefits of contextual variability during encoding: increasing the variety of effective retrieval cues and therefore greater likelihood of matching an unknown retrieval context, desirable difficulty in retrieving the first event during encoding of the second event, or some change in the way neural representations of the two events relate to one another.

We have some behavioral evidence that the first potential mechanism, encoding-retrieval cue match due to increased variety, does play a role in the benefit to item memory (Salan et al., under review). We found that purposely matching the retrieval context to one of the encoding contexts leads to similar performance for items encoded in the same context or variable context.

The second explanation, that difficulty in study-phase retrieval (also called “reminding”) produces benefits to later retrieval, has been proposed and supported in studies of the spacing effect (Feng et al., 2019; Maddox et al., 2018). However, to our knowledge, this proposal has not yet been tested in a context variability paradigm.

The third explanation, differences in the neural representations that are encoded for more similar events compared to more dissimilar events, is the focus of the current project. The current project used a repetition paradigm, allowing us to create highly similar events (two presentations of an identical item within the same environment and in close temporal contexts) that we then manipulated to either match or differ in their cognitive goals (defined here as the encoding task). We expected, given earlier behavioral studies, that item recognition memory would be better for items encoded with differing cognitive goals (two distinct encoding tasks) than it would be for items encoded twice with the same cognitive goal (a single encoding task). If the encoding task affects the nature of the information included in the memory representation (Tulving & Thomson, 1973), we would expect that neural activity patterns would be more similar for items encoded within the same cognitive context than for those encoded with differing cognitive contexts. Given our behavioral findings that variable contexts (and therefore variation in the representations) improve item memory, the similarity of the neural representations would then negatively predict item memory. As reviewed below, this finding would be inconsistent with the majority of existing findings regarding memory representations using fMRI pattern analyses. Instead, we might find that the relationship between neural representations and memory success depends on the cognitive goals during encoding, as suggested above.

1.2 Repetition and Neural Representations

Repeated studying of an item-to-be-learned has long been known to improve memory for that item (Ebbinghaus, 1913). However, the relationships between representations of repeated events stored in episodic long-term memory are as yet unknown. For example, does repetition of a prior event re-activate the representation for the original event and update it? Or is the repetition encoded as a novel event and linked to the prior event? If both types of representations are formed, which one provides a greater benefit to memory retrieval?

Many behavioral models of episodic memory propose that each event is encoded into a separate, unique, trace (e.g., Gillund & Shiffrin, 1984; Hintzman, 1988; Murdock, 1997; Nadel et al., 2000; Nosofsky, 1988). Most models also allow for the unique traces to form associative or semantic links to any related earlier events. At least one class of models predicts that a single trace is encoded for all repeated events occurring within the same context, known as differentiation models (Criss, 2006; Shiffrin & Steyvers, 1997). However, REM (Retrieving Effectively from Memory) also allows for differentiation of the expected single trace to be blocked by a change in context, thereby creating a second, separate, trace. Unfortunately, the circumstances under which repetitions will lead to either a differentiated single trace or separate traces are not yet known. Criss (2006) proposed that separate traces might be induced by manipulating encoding tasks that refer to distinct item properties, referencing separate definitions of words (e.g., riverbank vs. money bank), or manipulating temporal context. Therefore, it appears that REM would predict that items repeated within the same context would lead to the creation of a single trace for those events whereas items repeated within sufficiently variable contexts would result in multiple traces.

The proposal that each event is stored in a unique trace, no matter its relationship to earlier events, is consistent with the principle of "pattern separation". Pattern separation is the process by which two highly similar events form representations that are no more similar to one another than the representations formed by two very different events (Santoro, 2013). It is believed to result from the cellular and connective architecture of the hippocampus (Rolls, 2010). Several existing computational theories of hippocampal function incorporate pattern separation mechanisms during encoding and some empirical work also supports this mechanism (for a review, see Yassa & Stark, 2011). If similar events lead to representations that are orthogonal, producing the same outcome as distinct events whose representations are orthogonal, we should find no difference in representational similarity when repetitions occur in the same context or in variable contexts. Alternatively, if similar events lead to differentiated representations (rather than orthogonal representations, e.g., Favila et al., 2016), we should find that increased similarity between events (same context repetitions) produces more dissimilarity in hippocampal representations than do variable contexts.

Prior fMRI studies have examined the voxel-level neural patterns associated with repeated events using RSA. In RSA, the specific BOLD response in each individual voxel is measured and extracted across a region of interest. This pattern of BOLD signal across voxels can then be compared to a pattern of BOLD signal across voxels during a different event. For the current study, these two patterns are the first and second presentations of a particular to-be-remembered item. The overall similarity of the two patterns is then measured as a correlation and collated across a particular condition (e.g., all remembered items and all forgotten items). Analysis via RSA provides the most "representation-like" data that can currently be collected noninvasively from healthy human participants.

1.3 Increased Item-Level Similarity Across Repetitions Sometimes Benefits Memory

Of the existing studies that examine neural representations using RSA, relatively few have related the voxel-level patterns to later memory retrieval. Among those studies that have, most find that similarity in neural patterns across repetition benefits later memory retrieval of that item. One of the earliest relevant studies, by Xue and colleagues (2010), tested representational similarity during repeated encoding of words in an fMRI paradigm and measured subsequent memory. During scanning, participants made living/ non-living judgments in response to familiar words, each of which was presented 3 times with the same task. Memory was then tested with a free recall paradigm. Within-item pattern similarity (across each word's three presentations) was greater than between-item pattern similarity (across distinct words in the list) overall. Importantly, the difference between within-item and between-item similarity was significantly larger for words that were subsequently recalled than for words that were subsequently forgotten. This effect was found in the left dorsolateral occipital cortex, bilateral middle temporal gyrus, and bilateral inferior frontal gyrus. No significant effects were found in the hippocampus.

A number of other studies have produced similar findings to Xue et al. (2010) using distinct paradigms. A study of representational similarity across repetitions of an identical item as compared to presentation of a slightly altered item was designed to assess possible reactivation of the earlier event (van den Honert et al., 2016). Neural pattern similarity during the first presentation (e.g., a full-color scene) and the second presentation (e.g., the same scene in greyscale) was greater for items that were later successfully recognized as having been presented in the form of two similar images rather than a single repeated image. This effect occurred in both parahippocampal cortex and the hippocampus. The authors argued that increased pattern similarity of the two events indicates reinstatement of the first presentation experience during the second presentation.

Pattern similarity has been found to correlate with learning of novel stimuli (rather than episodic memory of familiar stimuli as in the studies reviewed thus far). Two studies used Korean characters as stimuli for non-Korean-literate participants in order to measure learning across multiple exposures (Lu et al., 2015; Qu et al., 2017). EEG pattern analyses (Lu et al., 2015) indicated greater within-item spatiotemporal pattern similarity for subsequently remembered items across three repetitions in the time window 500-656ms after stimulus presentation in the right frontal region and in a 547-688 time window in the left posterior region. An effect consistent with the earlier right frontal finding was found in a later EEG study that used spatiotemporal pattern analysis to examine subsequently remembered vs. forgotten faces (Feng et al., 2019). Lu and colleagues concluded that reactivation of the existing memory trace for the same item elicited higher within-item similarity across repetitions. A similar paradigm to Lu et al.'s learning of novel logographic words was later conducted with fMRI methodology and found that pattern similarity in inferior frontal gyrus (pars opercularis) and the fusiform gyrus was associated with successful learning (Qu et al., 2017).

Finally, Ward et al. (2013) found that higher pattern similarity across repetitions of the same stimulus predicted better subsequent recognition memory but also investigated the effect of spaced repetition. In this study, color images of scenes were each presented twice, and participants were asked to judge whether the scene was indoor or outdoor. After encoding, participants were given a surprise recognition test and asked to judge both studied and unstudied images as old or new using a confidence rating scale. The results indicated that higher pattern similarity across repetitions of the same image reliably predicted later recognition in lateral occipital cortex (LOC, known to represent visual characteristics), lingual gyrus, and middle temporal gyrus.

1.4 Decreased Item-Level Similarity Across Repetitions Sometimes Benefits Memory

Although the majority of studies investigating representational similarity across repetitions and subsequent memory performance find that increased similarity benefits memory, at least two studies have reached the opposite conclusion: that dissimilarity across repetitions benefits memory. The first of these findings is similar to the Xue, Ward, and other findings reviewed above in section 1.3 except that it investigated the effect of repeated retrieval trials rather than repeated encoding (Karlsson Wirebring et al., 2015). The second finding examined working memory performance rather than long-term memory performance (Veldsman et al., 2017). After describing each finding, we will explore potential explanations for its divergence from the studies described in section 1.3.

Extensive prior literature has revealed that repeated memory retrieval (sometimes called “the testing effect”) is more beneficial than repeated memory encoding (see Roediger & Butler, 2011 for a review). In particular, Karpicke and Roediger (2007) revealed that repeated testing of previously recalled information (i.e., information that has already been successfully “learned”) improves later memory retention compared to repeated studying of prior recalled information. The Karlsson Wirebring et al. study (2015) investigated how BOLD activity changes across repeated retrieval attempts and how these changes contribute to later retrieval. Swedish-speaking participants were initially asked to study 60 Swahili-Swedish word pairs presented for 5s each over 10 study trials for each pair prior to repeated retrieval practice (during which fMRI scanning was conducted). Surprisingly, within-item pattern similarity in right posterior parietal cortex was **lower** across repeated retrieval for items that would be remembered on the final memory test than for items that would later be forgotten. In other words, long-term retention was associated with less pattern similarity in right posterior parietal cortex across retrieval repetitions. This is the opposite of what was found by Xue et al. (2010) albeit in right parietal cortex rather than left occipital lobe, bilateral middle temporal gyrus, and bilateral inferior frontal gyrus. The authors interpreted this finding as indicating that repeated retrieval led to semantic elaboration of representations, which reduced neural pattern similarity and facilitated long-term retention. Karlsson Wirebring and colleagues' (2015) study might indicate that repeated retrieval has distinct mechanisms from repeated encoding that led to subsequent memory performance. It might also indicate that the extensive study trials (10 exposures to each pair) **preceding** the measures of representational similarity affected the outcome. For example, those word pairs might be transitioning from episodic storage to semantic storage. In contrast, the Xue et al. (2010) study had only two study exposures prior to measuring representational similarity.

The second study to find dissimilarity benefits in memory investigated working memory capacity for recognizable objects as compared to unrecognizable objects (warped versions of the original images; Veldsman et al., 2017). Recognizable objects produced more **variable** patterns across presentations and higher working memory accuracy than did unrecognizable objects in several occipital and parietal regions of interest (ROIs), including LOC. The authors attributed their pattern analysis findings to the opportunity to invoke deep processing via "rich contextual associations" for recognizable objects but not unrecognizable objects (Veldsman et al., 2017, p. 142). They then posit that these associations are highly variable from trial to trial based on earlier work by Bower and colleagues (1975). This explanation is similar to the semantic elaboration proposed in the Karlsson Wirebring paper (Karlsson Wirebring et al., 2015). It should be noted that memory accuracy in the Veldsman et al. study (2017) was based on ongoing maintenance (working memory) rather than retrieval from unconscious storage (episodic memory), as opposed to all other studies reviewed above.

1.5 Increased Global Similarity Across Items in Cortex Benefits Memory

Other studies that have used RSA to investigate subsequent memory measured global similarity rather than within-item similarity. All of the RSA studies reviewed thus far compared the pattern of BOLD signal across voxels during encoding of an item in its first presentation to the pattern produced by the same item in later presentations. In contrast, global pattern similarity compares neural patterns by collapsing across all items (sometimes within a particular category) rather than comparing neural patterns produced by the same item. The conclusions from studies that find global pattern similarity predicts memory retrieval are differ from those that find individual item pattern similarity predicts memory retrieval. In particular, such a finding clearly conflicts with the Xue study (2010) because it treated global pattern similarity as the baseline to which item similarity should be compared.

Global pattern similarity has been studied in relation to episodic memory and category identification. LaRocque and colleagues (2013) measured categorical pattern similarity during a fixation-cross monitoring task and therefore incidental memory encoding. Their findings indicate that greater similarity in parahippocampal cortex and perirhinal cortex of an object picture to other items within its category (e.g., faces, body parts, or inanimate objects) than to other categories predicted successful recognition of that item. A recent study replicated this result and found that cortical pattern similarity across concept exemplars predicted memory for a specific exemplar, attributing this to increased familiarity signal (Wing et al., 2020). Although each item was repeated within these experiments, the individual item repetitions were not compared to one another but rather only to the other items in that category or all items from distinct categories. Note that the LaRocque study (2013) found the reverse pattern in the hippocampus, such that a more unique voxel pattern in the hippocampus in response to an item (compared to other items in its category) predicted successful recognition memory (see section 1.6).

Another study using global pattern similarity as a measure found that increased similarity of a studied word to all other words presented during encoding predicted recognition confidence at retrieval (Davis et al., 2014). This differs slightly from the LaRocque study which compared within-category similarity to other-category similarity. The results also differed from the LaRocque and colleagues' study in that Davis and colleagues showed increased global pattern similarity predicted memory in both medial temporal lobe (MTL) cortex and the hippocampus, rather than that dissimilarity in the hippocampus predicted memory success.

1.6 Dissimilarity in the Hippocampus May Support Memory

As noted above, although the LaRocque study (2013) found that global pattern similarity in cortex supported memory retrieval, they found that global dissimilarity in the hippocampus supported memory retrieval. This dissociation fits with proposals that the hippocampus is specialized for pattern separation (described in section 1.2).

Similar conclusions regarding representational dissimilarity in the hippocampus were reached by Favila et al. (2016), although it should be noted that this study did not investigate subsequent memory. Participants learned face-scene associations to 100% accuracy in the study phase. During fMRI scanning, scenes were presented individually in order to investigate their representational similarity. Similar scenes (e.g., barn 1 and barn 2) that had been presented with the **same** face during encoding produced the most **dissimilar** patterns in the hippocampus. This is surprising from a cognitive perspective because similar scenes paired with the same face did not require differentiation from one another in order to learn the scene-face associations to criterion. The authors concluded that the unexpected finding of reduced representational overlap in the same face condition might be explained by hippocampal differentiation. That is, in the same face condition, when “bridge 1” was shown, the similar scene (“bridge 2”) would also be activated because of the presentation of the face paired with both bridges. This likely resulted in highly overlapping patterns of activation in the same-face condition on initial presentations. The authors proposed that the hippocampus responds to this overlap by reducing interference between those similar scenes, thereby driving the representations of those scenes apart from each other. Although this experiment provides an example of how hippocampal patterns might show evidence of pattern separation, the paradigm used in this study did not compare remembered to forgotten items and therefore cannot reveal the types of representations that predict later memory.

1.7 Effects of Context Variability on Source Memory

In addition to studies of simple repetition, two studies have investigated how manipulation of encoding conditions or context affects the representations of repeated events in memory. Both of these studies associated representational similarity with source memory (i.e., memory for the context within which an item was studied) rather than item memory (i.e., memory that a particular item was studied) and therefore differ from the current study. To our knowledge, no prior study has manipulated the context within which memory encoding occurs in order to determine how this cognitive factor might drive the relationship between neural patterns and item memory.

The goal of a study by Kim et al. (2019) was to assess whether context information from an initial event was reactivated during a second occurrence of that event. When analyzing item-level representational similarity with respect to source memory accuracy, they found that increased item pattern similarity in LOC between the initial encoding phase and repetition phase predicted **poorer** source memory performance.

Sievers and colleagues (Sievers, Smith, et al., 2019, preprint not peer-reviewed) also investigated how changes in context affect memory for that context information and reached the same conclusion. They predicted that higher pattern similarity across item repetitions in variable contexts would lead to poorer memory for those contexts. The study used famous names, each of which was presented four times during the study phase. The “same task” stimuli were presented 4 times within the same list, using the same encoding question. The “different task” stimuli were presented once on each of the 4 lists and thus studied using 4 different encoding questions. Participants were then tested using a recognition task with context judgments. Although old/new recognition judgments were collected, there were too few missed items to allow an fMRI analysis of correct vs. incorrect item memory. The behavioral analysis of item memory revealed poorer recognition memory in the same task condition than in the different task condition. This is consistent with behavioral findings in our lab (Salan et al., under review), although it should be noted that item spacing was not controlled in the Sievers study and therefore could be serving as a confound. In contrast to the item memory behavioral findings, the memory for the encoding questions, i.e., source or context memory, revealed poorer performance in the different task condition than in the same task condition. A whole-brain searchlight analysis of pattern similarity in the fMRI data identified a significant cluster in the posterior cingulate cortex that showed an interaction between context variability and source memory performance. Higher pattern similarity in this posterior cingulate region for **same** task items predicted better source memory performance. However, higher pattern similarity in this posterior cingulate region for **different** task items led to poorer source memory performance. In other words, reactivation of previously encoded representations from variable contexts negatively affected later memory for context whereas reactivation of previously encoded representations from the same context positively affected later memory for context. This pattern indicates that the nature of cognitive processing (i.e., the cognitive goal) influences the relationship between neural representations and later source memory retrieval.

The current study aims to determine whether such a pattern exists for item memory. The recognition test in our study (simple old/new judgments) does not require retrieval of context information and can theoretically be completed using familiarity for the item itself. Therefore, finding that context variability affects the relationship between memory representations and recognition success (regardless of whether context information is retrieved) broadens the circumstances under which cognitive factors can be seen to influence neural representations. Such a finding would also provide neural evidence that the context of an event can change the information encoded about an item, as proposed by the encoding specificity principle (Tulving & Thomson, 1973). We predicted that items repeated in the same context would show increased similarity in neural representations if they are later remembered as compared to those that are later forgotten. However, we predicted that items repeated in variable contexts will show decreased similarity in neural representations if they are later remembered as compared to those that are later forgotten. We expected to find this pattern of results in MTL cortex (i.e. parahippocampal cortex and perirhinal cortex) and LOC. Based on the findings by Favila and colleagues (2016) we hypothesized that the hippocampus would demonstrate differentiation among similar events, such that repetitions in the same context would result in reduced hippocampal pattern similarity as compared to repetitions in variable contexts. In both the same context and variable contexts, we expected that reduced hippocampal pattern similarity would predict better item memory.

2.1 Materials & Methods

2.2 Participants

The number of participants necessary to show a behavioral difference between the Same Context and Variable Context conditions (estimated based on data from a prior study in our lab with a similar manipulation in G*Power 3.1.6, Faul et al., 2007) was determined as 30 in order to achieve 80% power. Prior experiments with similar designs and analysis approaches have found significant RSA results with sample sizes ranging from 18 to 22 participants (LaRocque et al., 2013; Ritchey et al., 2013; Ward et al., 2013; Xue et al., 2010). We chose to collect at least 30 participants with usable fMRI data (i.e., with a sufficient number of remembered/forgotten trials and without excessive head motion). 46 participants were recruited via advertisement to the community at Virginia Tech with 16 being excluded from analyses (for reasons described below) so that the final number of participants was 30 with usable fMRI data. Our exclusion criteria were posted on Open Science Framework as part of our pre-registration of the study, and all exclusion decisions were made prior to analysis of the fMRI data (https://doi.org/10.17605/OSF.IO/PZXKD). Of the 16 participants excluded, 10 participants were excluded due to poor memory performance ($d' < 0.75$), 2 participants did not complete the experiment, 1 participant was excluded due to a technical issue resulting in missing memory test data, and 3 further participants did not meet our threshold for the minimum number of trials in each analysis bin (20, excluding movement outliers and trials without behavioral responses during scanning). Movement outlier trials were identified via the Artifact Detection Tools (RRID:SCR_005994) plugin in SPM (thresholds: z = 5, movement = 0.5, and rotation = 0.005).

Any participants who had uncorrected visual deficits, contraindications for MRI scanning, and permanently attached or implanted metals were excluded from the current study. Only participants who are fully vaccinated for COVID-19 were eligible to enroll. The age range of the participants whose data were included in the analyses was between 19 and 44 years (M = 27.47, 13 female). Of 46 participants we recruited, 35% of participants were White, 11% of participants were Black, 39% of participants were Asian, 13% of participants were Latinx, and 2% of participants identified with more than one category. Handedness was not considered when recruiting participants, but it was measured via a simplified version of the Edinburgh Handedness Inventory (Oldfield, 1971). Of the 30 participants included in the analysis, 27 reported writing with their right hand and 3 with their left hand. The 3 lefthanded participants all reported some degree of ambidexterity for non-writing activities. Participants were compensated monetarily for participating. The study was approved by the Human Research Protection program at Virginia Tech via external review from BRANY (Biomedical Research Institute), file # VT18-1077-568(TRX). Informed consent was obtained for all participants in the study.

2.3 Materials

Image stimuli were selected from the Bank of Standardized Stimuli (BOSS) (Brodeur et al., 2010, 2014). Images for the current study were hand selected from those that were either always recognized by participants in the normalization study (0% responded with "Don't Know Object") or that fewer than 15% of normalization participants were unable to name successfully ("Don't Know Name"). A total of 416 images were chosen, excluding any with high conceptual similarity or similarity in their verbal label to other selected items. Half of the 416 images were randomly selected for each participant to serve as studied items while the other half were presented as unstudied items during the retrieval phase.

The encoding questions used to differentiate the contexts were drawn from a set of distinctive semantic encoding questions previously used in our lab. We chose two questions that both require processing of the identity of the item in the image but that each direct the participant's attention to a different characteristic of the item and a different environment in which to imagine the item. An abbreviated version of the question appeared with a corresponding scale on each image trial as follows: "Is this item useful on a deserted island?" and "Could you carry this item a long distance?". In order to encourage the participants to think carefully about each question, we began each context block with self-paced presentation of longer, more detailed versions of the questions and accompanying rating scales (see Table 1). Participants were instructed to think about the detailed scenario when responding to each image.

2.4 Behavioral Design

The experiment involved a study phase and test phase, with 8 to 10 days (M = 9.63) delay between the two phases. The study phase trials consisted of object images presented with an encoding/processing question for each image. All images were studied twice. The test phase consisted of object images (half previously studied and half novel) being presented one at a time with the participant asked to judge whether they had previously seen the object in the experiment. The delay of 8 to 10 days between study and test phases was chosen based on a pilot behavioral study. The goal of the delay was to adjust memory accuracy to the point that approximately equal numbers of items were remembered and forgotten, thus allowing robust trial numbers for the fMRI analysis of future item memory.

Repetition context was manipulated during the study phase. Items studied in the "Same Context" condition were presented twice using an identical encoding question, with both questions (see Table 1) appearing equally often in this condition. Items studied in the "Variable context" condition were presented once with each question, with each question occurring equally often as the first of the two seen with a given item. Context was defined as the continuous block of trials within which the same encoding question was presented. The study phase consisted of 9 context blocks such that the encoding question changed only between each block. In order to control repetition spacing and counterbalance condition order, context blocks varied between as few as 13 trials and as many as 52 trials. When a new block began, participants were shown a preview of the full encoding question and the corresponding rating scale that would be used on the subsequent trials.

Both the assignment of encoding question to blocks and the order of conditions were counterbalanced across participants. A custom MATLAB script was used to randomize the assignment of images to studied or unstudied items, Same or Variable Context condition, and position of each repetition on the study list for each participant. This script also controlled repetition spacing such that the second presentation of each image (in both conditions) was programmed to occur an average of 12 intervening trials after its first presentation (minimum spacing = 8 trials; maximum spacing = 16 trials). The spacing parameters were identical in the Same Context and Variable Context conditions. The actual calculated repetition lag in each condition for the final data set averaged 11.96 trials in the Same Hit condition, 11.95 trials in the Same Miss condition, 11.98 trials in the Variable Hit condition, and 11.97 trials in the Variable Miss condition (all standard deviations ranged from 0.3 to 0.4). Spacing was not held constant because that would require the items to be repeated in the identical order. We allowed spacing to vary within the parameters described above in order to prevent participants from encoding a particular stimulus order or relationships across stimuli as might occur if image order remained the same from the first to second presentation.

Encoding Question	Abbreviated Question	Rating Scale		
		1	2	3
Imagine that you were stranded on a deserted island with no other people and only the natural resources of the island to help you survive. In that scenario, if you were to find the object shown in the picture on the island would that object be useful to help you survive?	Is this item useful on a deserted island?	Not useful	Somewhat useful	Essential
Imagine that there is an emergency that requires someone to carry the item shown in the picture across a large field to the other side. You could carry it on your back, in your arms or in a backpack if that is helpful. If you were the only person available to do it would you be able to carry the object?	Could you carry this item a long distance?	Impossible	Possible but hard	Very easy

Table 1. *Long- and short-version encoding questions presented during the study phase with accompanying rating scale.*

2.5 Experiment Procedure

Participants were pre-screened for MRI safety and COVID-19 vaccine status prior to arriving at the MRI scanner. The MRI facility was cleaned and sanitized according to covid protocols in between participants, as approved by the IRB. Participants and experimenters were required to wear masks at all times, except that the subject was permitted to remove their mask while in the scanner room.

The instructions for the task informed participants that they would view a series of object images, with a specific question being asked about each object. They were told that they should think about the object in the image and enter their response on each trial, even if they had seen it previously. Participants were not told that they would be asked to remember the items for an eventual test. Each participant completed a series of practice trials prior to the encoding phase (with items not used in the actual experiment) to familiarize them with the encoding questions, trial timing, and response buttons.

The experiment was programmed using *Presentation* software (Version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA) was used for both the study phase and test phase. Each trial was synchronized to the onset of a scanner pulse. A trial began with presentation of an object image and the abbreviated encoding question for that block (Figure 1). The stimulus remained on the screen for 2s, after which a fixation cross replaced the object image while the question and response scale remained on the screen for an additional 2s. Participants were asked to make their response ("1", "2", or "3", see Table 1) to the question during this 2s interval. Participants were told that this judgment should be their own opinion. The intertrial interval (ITI) between study trials averaged 6s (including the response period), with a minimum of 4s and maximum of 10s. After the response period, the ITI was filled with presentation of single words (one per second) that related to the encoding question for the current block. The purpose of this filler was to engage participant attention and prevent effortful rehearsal of the studied items while also maintaining the ongoing context associated with each encoding question. These filler items appeared in random order and repeated across the experiment. Participants were asked to read these words as they awaited the next trial but not make any button presses in response. After functional scanning was complete, participants received their first session compensation and reminders about the schedule for their second session.

Participants returned for an unscanned memory test an average of 9.63 days after the encoding session. During the test, each of 208 studied images and 208 new images were presented individually in a random order with the retrieval question “Have you studied this image?” at the top of the screen. The participants were asked to press the buttons “f” or “j” to answer either “Yes/Old” or “No/New”. The test trials were self-paced such that the images were presented on the screen until the participant entered their response. After the participant’s response, a fixation cross appeared for 500ms before the next image was presented. Participants received additional compensation and a copy of their structural MRI at the second experiment session.

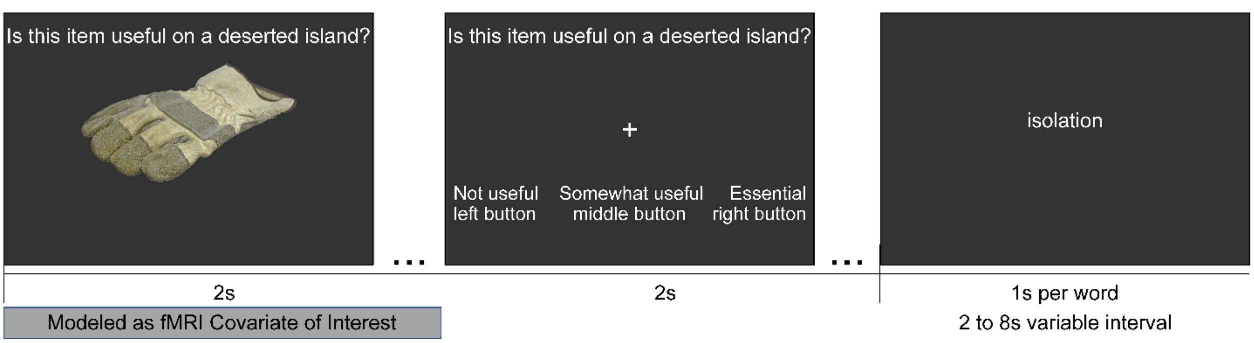

Figure 1. *Sample study trial.*

2.6 fMRI Design

2.6.1 Intertrial Intervals (ITIs)

Although best practices for intertrial intervals during fast event-related fMRI designs are well established (variable intertrial intervals that can average as few as 4s), the requirement to model each trial individually in order to extract trial-specific BOLD signal for RSA suggests that a different approach to the intertrial interval may be optimal. Recent papers have investigated whether short, variable, intervals are feasible when single trials will be modeled. Although Zeithamova and colleagues (2017) proposed that longer, non-variable ITIs are beneficial for studies modeling individual trials, a close examination of their data reveals that modeling with a Least-Squares Separate (LSS) model (as described above) did not produce better results at longer ITIs. An earlier study also found that LSS models performed equally well given jittered ITIs of 0 to 4s through 6 to 10s (Mumford et al., 2012). Abdulrahman and Henson (2016) used simulation data to assess the optimal data collection parameters for which individual trial data could be successfully classified. They found that, across a range of trial variability and scan noise parameters, the optimal range of ITI for LSS-N models was greater than 2s but less than 10s. Even when trial variability and scan noise were high, there was no apparent benefit to an ITI longer than 4 to 6s. Therefore, we used an ITI that averaged 6s, ranging from 4 to 10s.

2.6.2 Within-Run vs. Between-Run Comparisons

Multiple runs, allowing communication with the participant and opportunities for rest within the scanner between each run, were conducted for the current study given that the encoding phase was approximately 55 minutes in length. fMRI data are known to be more strongly correlated within a single run (an uninterrupted echo-planar imaging sequence) than across multiple runs. Studies examining RSA methodology suggest that either within-run correlations or between-run correlations can be appropriate, however, within-run correlations should not be compared to between-run correlations (Dimsdale-Zucker & Ranganath, 2018). Simulation studies of fMRI indicate that the choice of within-run or between-run comparisons can affect the Type I error rate unless either the stimuli are completely randomized in their presentation or the correlations between voxel patterns are restricted to within-trial-type similarity comparisons only (Mumford et al., 2014). Although our study design did not permit total randomization of the trial order, due to the need to block items by context and inability to control the distribution of hit and miss trials, we analyzed voxel patterns exclusively within-trial-type. That is, the voxel pattern resulting from a given image stimulus (e.g. the work glove in Figure 1) was only correlated with the voxel pattern resulting from the repetition of that same image. By definition, these two patterns result from the same experimental conditions: Same Context remembered, Same Context forgotten, Variable Context remembered, and Variable Context forgotten. Mumford and colleagues (2014) demonstrated that Type I error rates were at the desired level of 0.05 or below for within-trial-type comparisons for blocked designs that used within-block analyses.

Temporal autocorrelation, the similarity of non-cognitively driven signals at close points in time compared to those at further temporal distances, is an important consideration in RSA studies. One recent estimate of the effects of temporal autocorrelation in RSA found that 4 to 5 trials before and after each item are substantially affected by autocorrelation (Dimsdale-Zucker & Ranganath, 2018). Although we implemented spacing from 8 to 16 trials between repetitions that will be correlated, based on that estimate, we also computed a temporal correlation matrix from our first participant's data (using a hippocampal mask) in order to ensure that the effects of temporal autocorrelation in our data fell outside that range. The band of temporally-based differences in correlation ran approximately 20 TRs before and after each trial. The minimum number of trials between repetitions in our task was 8 and the average trial was 4 TRs long. Therefore, our analyses of interest used trials a minimum of 32 TRs separated in time. We concluded that this was sufficient separation to avoid the 20 TR effect of autocorrelation in the data.

2.6.3 1st-level GLM approach

Several approaches have been proposed for the first-level generalized linear model (GLM) analysis of individual participant data intended for RSA or multivoxel pattern analysis at the second level. The LSS model requires a separate GLM for each trial, within which only that trial is modeled as a covariate of interest. In terms of the covariates of no interest, LSS can either be constructed with separate covariates for each condition type (LSS-N with N for the number of condition types) or with a single covariate of no interest for all non-targeted trials (LSS-1). Two papers using a simulation approach agree that LSS-N models produce more accurate results for analysis of voxel patterns (Abdulrahman & Henson, 2016; Mumford et al., 2012). We are not aware of any existing papers that argue for an LSA or LSS-1 approach to modeling RSA data. Therefore, the current project was analyzed by constructing an LSS-4 model for each trial, represented by a stick function for the single TR during which the study image was visible, with four separate covariates of no interest for the remaining trials in each condition (i.e., Same Context remembered, Variable Context remembered, Same Context forgotten, and Variable Context forgotten). We also included covariates of no interest for head motion.

2.6.4 fMRI Acquisition Parameters

MRI data were acquired using a 3T Siemens Trio scanner equipped with a 12-channel phased array head coil at the Virginia Tech Corporate Research Center Human Neuroimaging Lab. Functional scans used a gradient echoplanar imaging (EPI) sequence (repetition time/TR = 2000ms; echo time/TE = 25ms; field of view = 192 mm); each volume had 35 sagittal slices, with a thickness of 3.0 mm and a starting distance factor of 25% (increased as needed to allow full brain coverage up to 50%), resulting in a voxel size of 3.0 × 3.0 × 3.0 mm. T-1 weighted structural images coplanar with the EPIs were acquired using an MPRAGE sequence (field of view = 243 mm; voxel size = 0.9 × 0.9 × 0.9 mm; number of slices = 208).

2.6.5 ROI Selection

Given existing knowledge of the regions involved in episodic memory encoding, we identified the parahippocampal cortex, perirhinal cortex, and hippocampus as our primary regions of interest for this study. These regions were defined anatomically using widely accepted visual markers (Buffalo et al., 2006) as described in prior manuscripts (Diana et al., 2008). In addition, based on a prior study (Kim et al., 2019) we used LOC activation as a measure of high-level visual object processing. As in the Kim et al. study, we used the Harvard-Oxford cortical atlas as the basis for a mask of LOC drawn on the MNI canonical brain. We then warped that canonical mask into each individual subject's native brain space, hand-checking the results for accuracy. The average size of each ROI mask in voxels is listed in Table 2.

Mask Size		M	SD
Hippocampus			
	Left	135.47	18.92
	Right	138.20	15.83
Perirhinal cortex			
	Left	117.23	22.82
	Right	117.93	29.87
Parahippocampal cortex			
	Left	116.27	22.41
	Right	105.13	24.20
Lateral occipital cortex			
	Left	489.50	46.65
	Right	459.90	38.25

Table 2. *Average number of voxels and standard deviation in each ROI mask.*

2.7 Analysis

This project was registered prior to data analysis at the Open Science Framework, publicly available at: https://doi.org/10.17605/OSF.IO/PZXKD, where links to the pre-registered analysis plan, fMRI data, behavioral data, and custom analysis scripts are available.

Any participant whose behavioral performance fell below a *d′* of 0.75 were excluded from further analysis. The primary behavioral measure of interest was hit rate, averaged across context condition (same vs. variable) for each participant and analyzed with a one-way repeated measures analysis of variance (ANOVA). Hit rate was chosen as the measure of interest given that the context manipulation during study does not apply to new items (as they have not been studied) and therefore only a single overall false alarm rate can be calculated.

Trial Numbers in RSA	M	SD	Minimum
Same Context			
Hits	48.97	12.12	20
Misses	55.03	12.12	37
Variable Context			
Hits	56.90	12.98	27
Misses	47.10	12.98	27

Table 3. *Average, minimum, and standard deviation of trial numbers included in RSA calculations for each context condition.*

SPM12 was used for pre-processing and first-level analysis of the fMRI data. Data were co-registered to correct for movement within a functional sequence, slice time corrected, and then realigned with a linear registration function to the high-resolution structural image. Participant data was maintained in native space rather than being normalized to a template brain. Minimal smoothing was applied (2mm full-width at half maximum smoothing kernel), which may increase signal-to-noise and accuracy of voxel-level pattern analysis without disrupting the integrity of the voxel pattern (Dimsdale-Zucker & Ranganath, 2018; Op de Beeck, 2010). The ART toolbox in SPM (Artifact Detection Tools, RRID:SCR_005994) was used to assess the quality of each participant's data, including identifying motion parameters to be included as covariates of no interest. Participants with insufficient usable trial numbers (due to either movement outliers or lack of behavioral responses) were excluded prior to calculating RSA correlations. A minimum of 20 trial pairs were included in each RSA analysis in each condition, with the average trial numbers across conditions shown in Table 3.

Following preprocessing, an LSS-4 modeling approach was applied to extract the BOLD signal corresponding to each behavioral trial. The GLM implemented the option "FAST" for pre-whitening rather than the default in SPM due to the fact that FAST minimizes temporal autocorrelation more effectively (Corbin et al., 2018; Olszowy et al., 2019). The vector of voxel values corresponding to each trial for each anatomically-defined ROI was extracted for RSA from the first-level GLMs using custom MATLAB scripts. For example, viewing of the "work glove" image in the Same Context condition, with a subsequent correct memory judgment, produced two vectors for each ROI (parahippocampal cortex, perirhinal cortex, the hippocampus, and LOC): WorkGlove_time1 and WorkGlove_time2. The Pearson correlation for each set of vectors then served as a data point in the Same Context, remembered condition for further statistical analysis within that ROI. Each Pearson correlation was Fisher-transformed before averages were calculated across the trials within a condition for each participant. Statistical assessment of condition-level correlation differences was performed with separate 2x2x2 repeated measures ANOVAs (context condition by hemisphere by memory outcome) for each ROI.

3.1 Results

3.2 Behavioral Results

Overall, participants successfully retrieved 51% (*SD* = 12%) of the items that were presented during the study trials while making false alarm responses to 12% of new items (*SD* = 8%). False alarm responses were not analyzed further because the manipulation of interest (encoding question) does not apply to new items. Participants correctly retrieved an average of 47% (*SD* = 12%; Figure 2) of the Same Context items, which were repeated with the same questions during study, and 55% (*SD* = 12%) of the Variable Context items, which were repeated with different questions during study. A paired sample t-test revealed that participants were significantly better at recognizing items from the Variable Context condition than items from the Same Context condition ($t_{(29)}$ = -7.65, p < .001; Figure 2). The average d' score was 1.30 with the minimum at 0.78 (all participants with d' below 0.75 were excluded based on our pre-registered criteria) and the maximum at 1.96 (*SD* = 0.34).

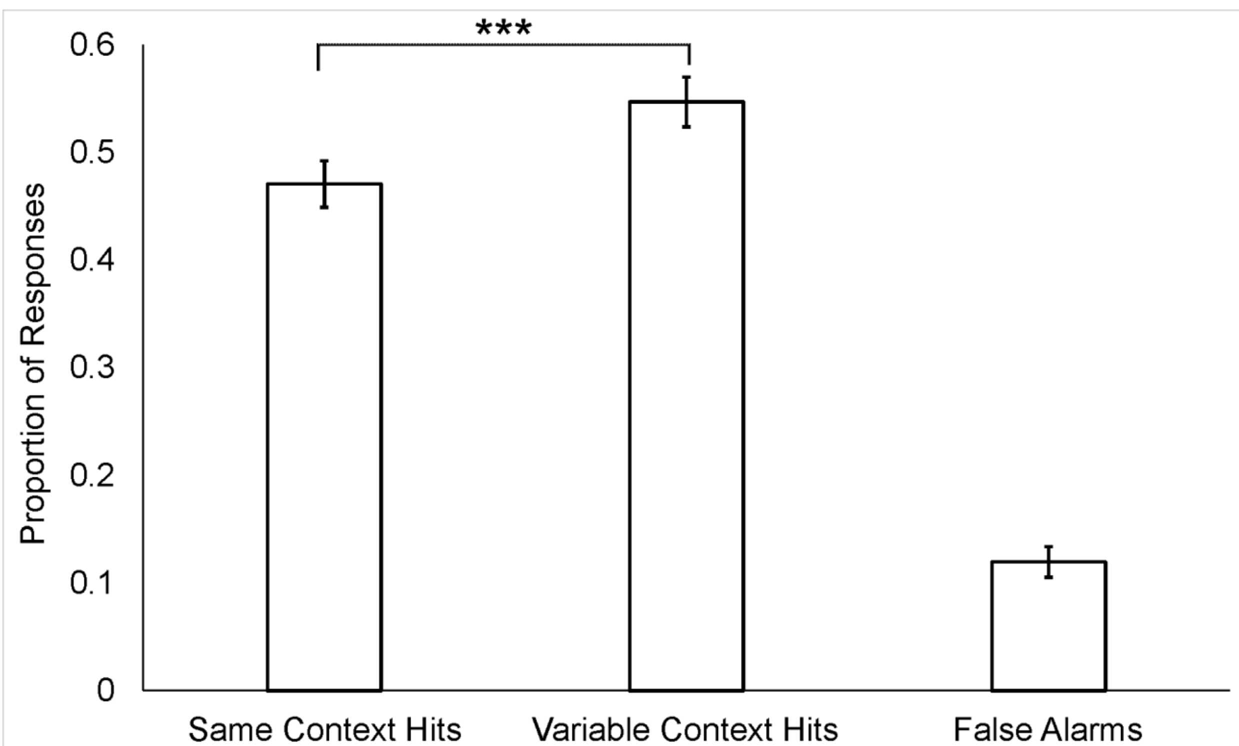

Figure 2. *Proportion of hits in the Same and Variable Context conditions and false alarms which do not differ by encoding condition. The error bars indicate the standard error.* *** $p < .001$

3.3 fMRI Results

3.3.1 Parahippocampal Cortex

A 2x2x2 repeated measures ANOVA was performed to assess the pattern of activation (Same vs. Variable Context by Remembered/Hit vs. Forgotten/Miss by Left vs. Right hemisphere) for each distinct anatomical ROI. Follow-up t-tests were performed to reveal condition-level effects in any significant interactions found by the ANOVA at an alpha level of .05. We predicted that MTL cortex, including parahippocampal cortex and perirhinal cortex, would show higher pattern similarity for the repeated items in the Same Context condition that were subsequently recognized but lower pattern similarity for repeated items in the Variable Context condition that were subsequently recognized. We did not predict any effects of hemisphere.

The ANOVA revealed a significant main effect of hemisphere ($F(1, 29) = 10.22$, $p = .003$, $\eta_p^2 = 0.26$). Right parahippocampal cortex showed significantly higher pattern similarity across the repeated items ($M = 0.11$) than left parahippocampal cortex ($M = 0.08$). All findings of differences in laterality were followed-up with an identical statistical analysis that included only right-handed participants (N = 27). The significant main effect of hemisphere was still found when all participants were right-handed, but the effect size was smaller ($\eta_p^2 = 0.22$).

There was no significant main effect of subsequent recognition accuracy ($F(1, 29) = 2.63$, $p = .12$, $\eta_p^2 = 0.08$). A main effect of context was found ($F(1, 29) = 7.43$, $p = .01$, $\eta_p^2 = 0.20$) indicating that pattern similarity across the repeated items was higher in the Same Context condition (M = 0.11), compared to the items in the Variable Context condition (M = 0.09) in bilateral parahippocampal cortex, however this main effect was qualified by a significant 2-way interaction between context and hemisphere ($F(1, 29) = 10.05$, $p = .004$, $\eta_p^2 = 0.26$). Follow-up paired-samples t-tests revealed a significant difference in pattern similarity based on encoding context (Same vs. Variable Context) only in left parahippocampal cortex ($t_{(29)} = 3.82$, $p < .001$) and not in right parahippocampal cortex ($t_{(29)} = 0.75$, $p = .46$), seen in Figure 3. In left parahippocampal cortex, pattern similarity was greater for items repeated in the Same Context condition (M = 0.09) than those repeated in the Variable Context condition (M = 0.07). The 2-way interaction between context and hemisphere was still found when only right-handed participants were included in the analysis, with the resulting effect size of the interaction being larger (η_p^2= 0.28) and the follow-up t-tests showing the same pattern.

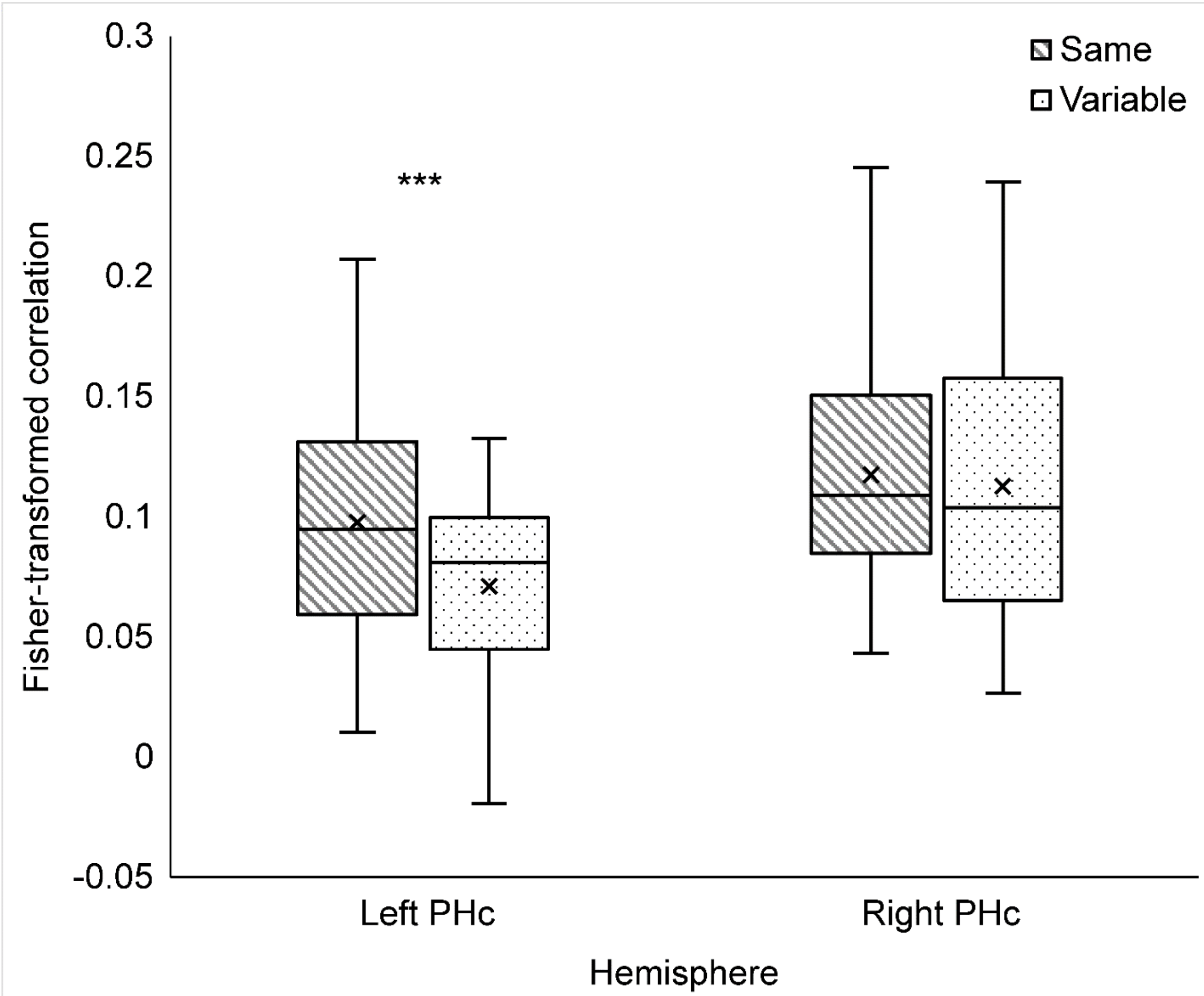

Figure 3. *The distribution of neural pattern similarities, as Fisher-transformed correlations, of left and right parahippocampal cortex (PHc) for the items repeated in the Same and Variable Context conditions. "X" indicates the mean value in each condition, boxes indicate the range of the inner quartiles, whiskers indicate the range of the outer quartiles, no range outliers were identified. ***p* $< .001$

Another significant 2-way interaction in pattern similarity was found between accuracy and hemisphere in parahippocampal cortex ($F(1, 29) = 6.72$, $p = .02$, $\eta_p^2 = .19$). Results from follow-up paired-samples t-tests revealed a significant difference in accuracy (hit vs. miss) in right parahippocampal cortex ($t_{(29)}$ = 2.90, p = .007; Figure 4). The neural patterns in right parahippocampal cortex across repeated items that were later successfully remembered (M = 0.12) were significantly more similar than for repeated items that were later forgotten (M = 0.11). In contrast, left parahippocampal cortex did not show a significant difference based on accuracy ($t_{(29)}$ = 0.37, p = .72). The 2-way interaction between memory accuracy and hemisphere was also found when only right-handed participants were included in the analysis, but the resulting effect size of the interaction was smaller (η_p^2= 0.14). The follow-up t-tests revealed the same pattern as the original analysis.

The predicted 2-way interaction between context and accuracy was not found (F(1, 29) = 0.10, p = .76, η_p^2 = 0.003). There was also no 3-way interaction between context, accuracy, and hemisphere in parahippocampal cortex (F(1, 29) = 0.65, p = .43, η_p^2 = 0.02).

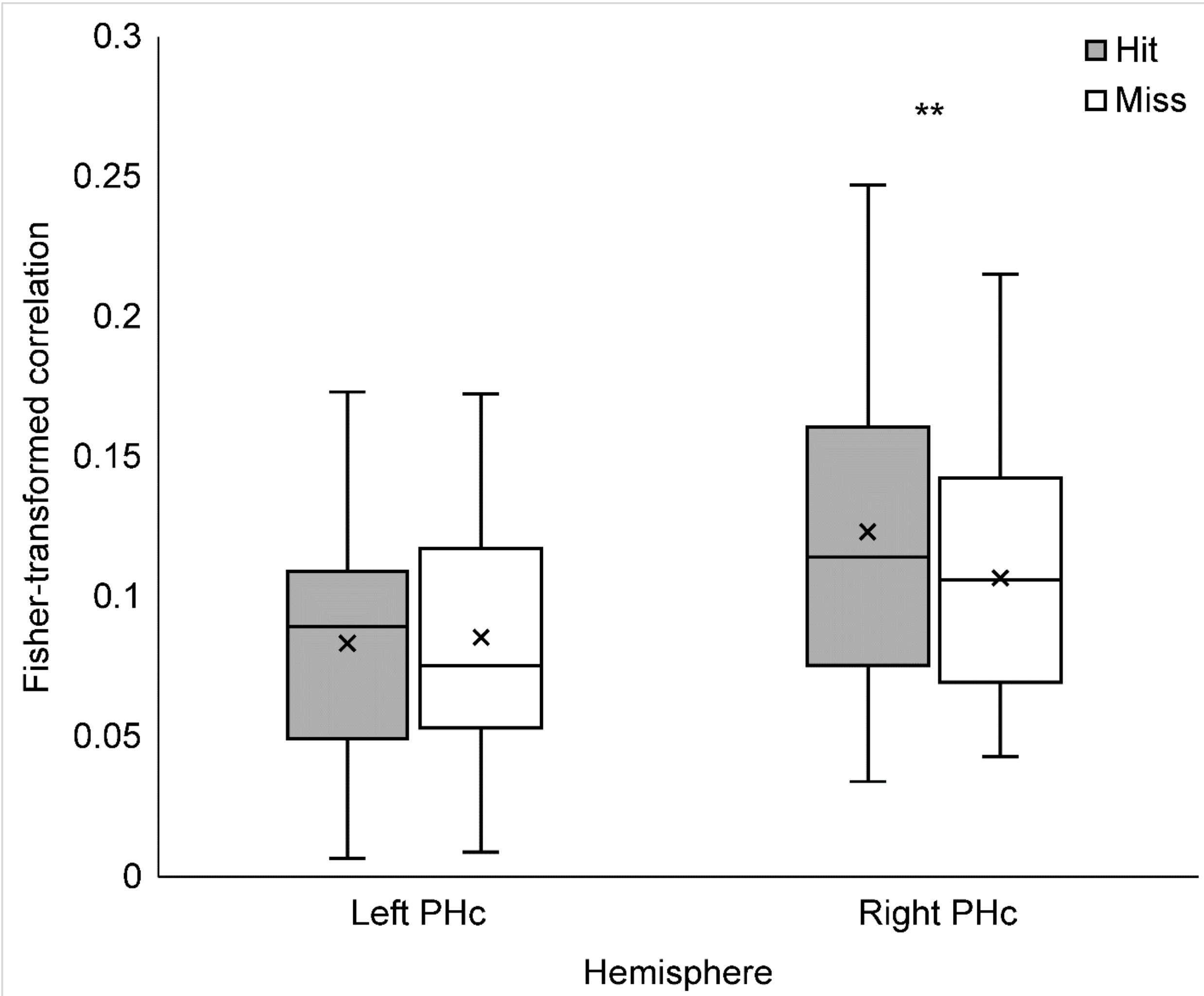

Figure 4. *The distribution of neural pattern similarities, as Fisher-transformed correlations, of left and right parahippocampal cortex (PHc) for the items later producing Hit responses vs. those that produced Miss responses. "X" indicates the mean value in each condition, boxes indicate the range of the inner quartiles, whiskers indicate the range of the outer quartiles, no range outliers were identified.* ***p* < .01

3.3.2 Perirhinal Cortex

Perirhinal cortex showed the same numerical and statistical patterns as parahippocampal cortex. Once again, the repeated-measures ANOVA revealed a significant main effect of hemisphere ($F(1, 29) = 19.66$, $p < .001$, $\eta_p^2 = 0.40$). Overall, right perirhinal cortex showed significantly higher pattern similarity across the repeated items ($M = 0.07$) than did left perirhinal cortex ($M = 0.04$). This significant main effect of hemisphere was still found when all participants were right-handed, but the effect size was smaller ($\eta_p^2 = 0.37$).

There was no main effect of subsequent recognition accuracy ($F(1, 29) = 0.24$, $p = .63$, $\eta_p^2 = 0.01$). A main effect of context was found ($F(1, 29) = 4.44$, $p = .04$, $\eta_p^2 = 0.13$) indicating that pattern similarity across the repeated items was higher in the Same Context condition ($M = 0.06$), compared to the items in the Variable Context condition ($M = 0.05$) in bilateral perirhinal cortex, however this main effect was qualified by a significant 2-way interaction between context and hemisphere ($F(1, 29) = 14.62$, $p < .001$, $\eta_p^2 = 0.34$). Follow-up paired-samples t-tests revealed a significant difference in pattern similarity based on encoding context (Same vs. Variable Context) only in left perirhinal cortex ($t_{(29)} = 4.16$, $p < .001$) and not in right perirhinal cortex ($t_{(29)} = 0.98$, $p = .33$), seen in Figure 5. In left perirhinal cortex, pattern similarity was greater for items repeated in the Same Context condition ($M = 0.06$) than those repeated in the Variable Context condition ($M = 0.03$). The 2-way interaction between context and hemisphere was still found when only right-handed participants were included in the analysis, with the resulting effect size of the interaction being larger ($\eta_p^2 = 0.39$) and the follow-up t-tests showing the same pattern.

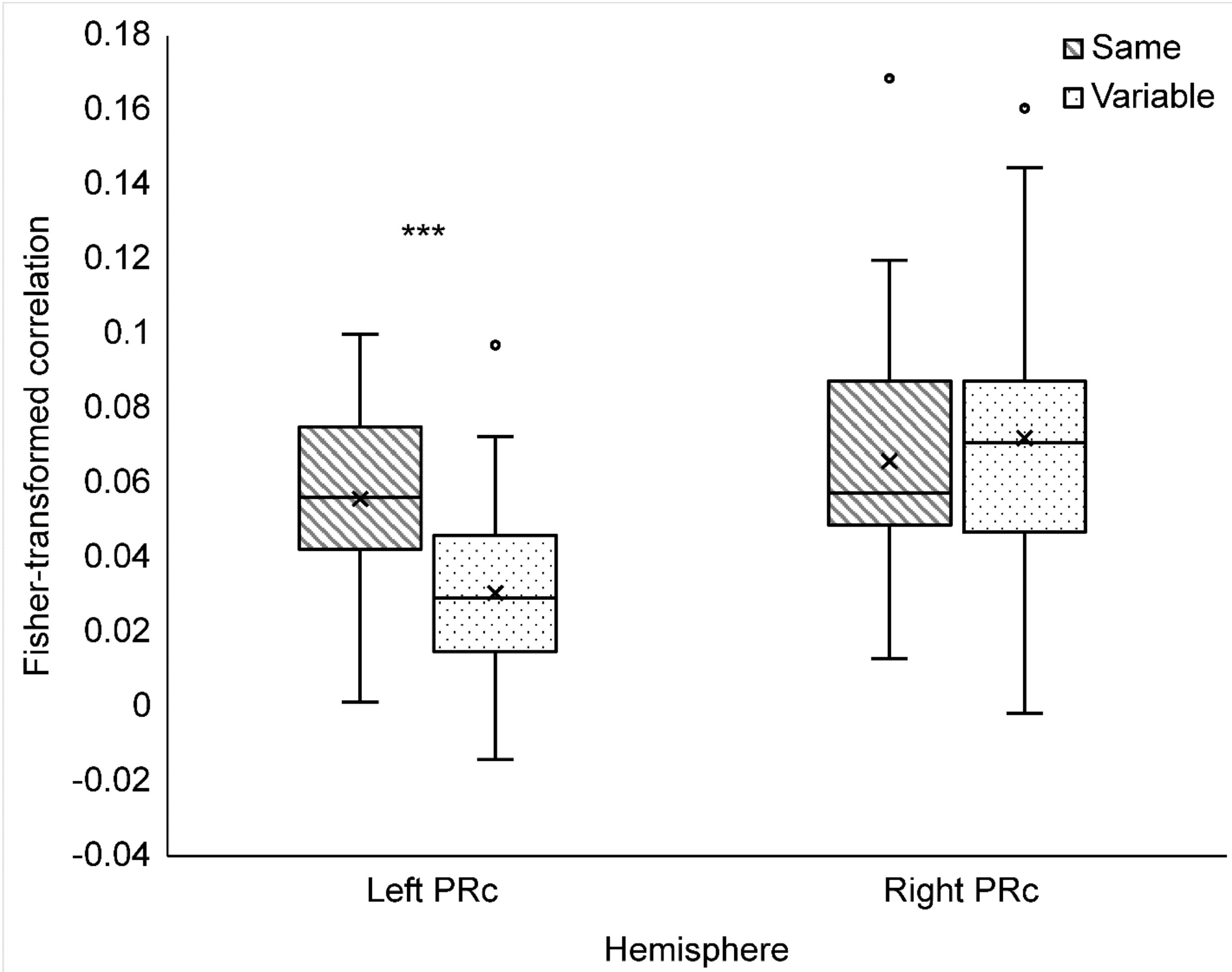

Figure 5. *The distribution of neural pattern similarities, as Fisher-transformed correlations, of left and right perirhinal cortex (PRc) for the items repeated in the Same and Variable Context conditions. "X" indicates the mean value in each condition, boxes indicate the range of the inner quartiles, whiskers indicate the range of the outer quartiles, range outliers are plotted as individual points.* *** $p < .001$

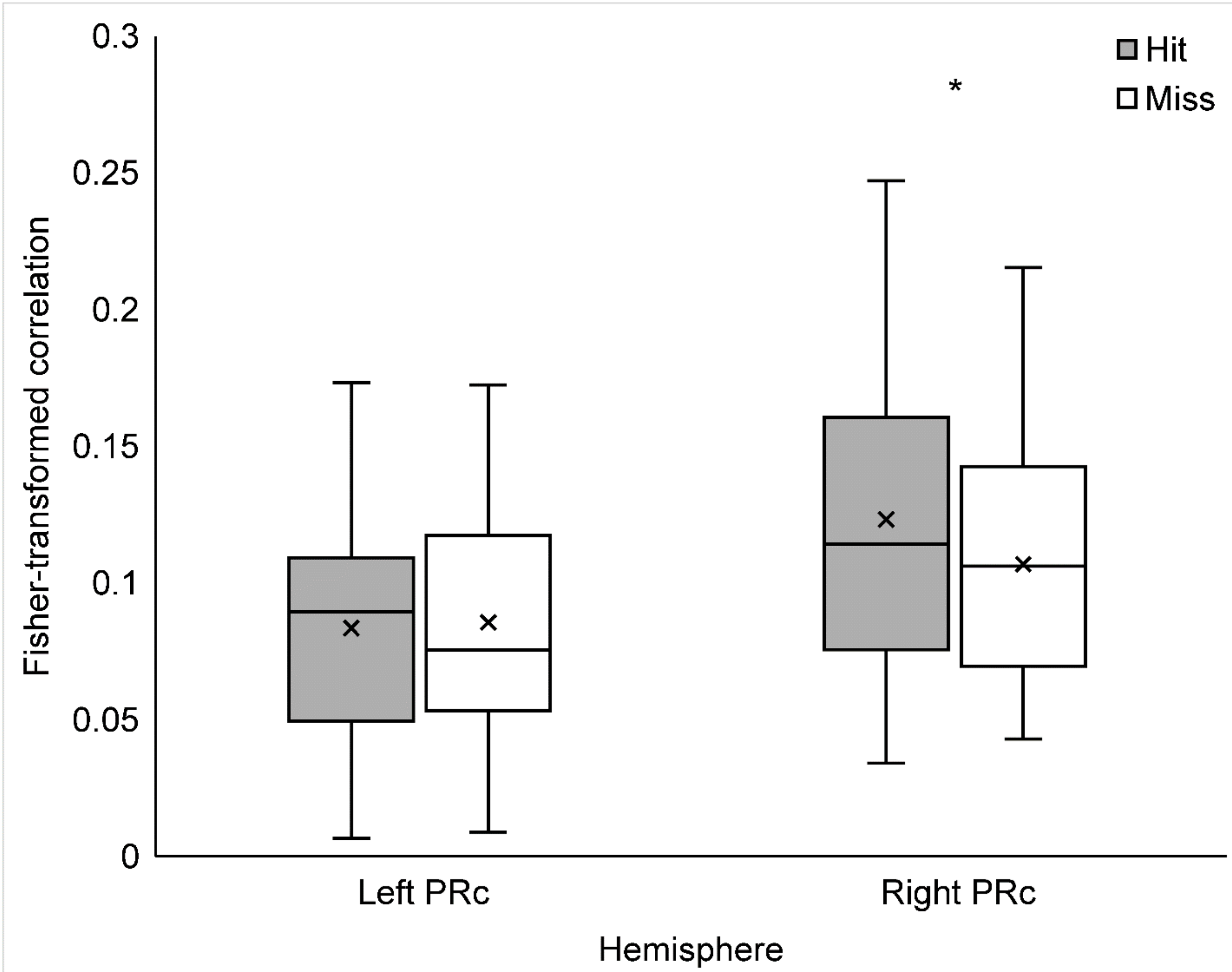

Figure 6. *The distribution of neural pattern similarities, as Fisher-transformed correlations, of left and right perirhinal cortex (PRc) for the items later producing Hit responses vs. those that produced Miss responses. "X" indicates the mean value in each condition, boxes indicate the range of the inner quartiles, whiskers indicate the range of the outer quartiles, and no range outliers were identified.* * $p < .05$ *Note that the statistical significance identified in this figure was not found when only right-handed participants were included in the analysis.*

Another significant 2-way interaction in pattern similarity was found between accuracy and hemisphere in perirhinal cortex ($F(1, 29) = 7.25$, $p = .01$, $\eta_p^2 = 0.20$). Results from follow-up paired-samples t-tests revealed a significant difference in accuracy (hit vs. miss) in right perirhinal cortex ($t_{(29)}$ = 2.34, p = .03; Figure 6). As in right parahippocampal cortex, the neural patterns in right perirhinal cortex across repeated items that were later successfully remembered (M = 0.07) were significantly more similar than for repeated items that were later forgotten (M = 0.06). Left perirhinal cortex also showed the same pattern as left parahippocampal cortex such that the left hemisphere did not show a significant difference based on accuracy ($t_{(29)}$ = 1.08, p = .29). However, the 2-way interaction between memory accuracy and hemisphere was not found when only right-handed participants were included in the analysis (F(1, 26) = 1.93, p = .18, η_p^2 = 0.07) and the follow-up t-tests did not show significant differences in either left or right perirhinal cortex between items that were later successfully remembered and items that were later forgotten.

The predicted 2-way interaction between context and accuracy was not found in perirhinal cortex (F(1, 29) = 0.17, p = .69, η_p^2 = 0.006). There was also no 3-way interaction between context, accuracy, and hemisphere in perirhinal cortex (F(1, 29) = 0.04, p = .84, η_p^2 = 0.001). Again, all of the statistical findings in perirhinal cortex paralleled the findings in parahippocampal cortex.

3.3.3 Lateral Occipital Cortex

LOC showed a unique pattern as compared to parahippocampal cortex and perirhinal cortex. The 2x2x2 repeated-measures ANOVA revealed three significant main effects and no interactions in LOC. The significant main effect of context (F(1, 29) = 55.13, p < .001, η_p^2 = 0.66, Figure 7) indicated higher pattern similarity across items repeated in the Same Context condition (M = 0.21) than items repeated in the Variable context condition (M = 0.18), regardless of memory accuracy or hemisphere. The significant main effect of accuracy (F(1, 29) = 10.00, p

= .004, η_p^2 = 0.26) indicated the items that were subsequently recognized produced higher correlations across the repetitions (M = 0.20) than did items that were subsequently missed (M = 0.19), regardless of context condition or hemisphere. Lastly, the significant main effect of hemisphere ($F(1, 29) = 29.52$, $p < .001$, η_p^2 = 0.50) indicated higher pattern similarity across repetitions in right LOC (M = 0.24) than in left LOC (M = 0.15), regardless of memory accuracy or context condition. This significant main effect of hemisphere was still found when all participants were right-handed, but the effect size was smaller (η_p^2= 0.46). We did not identify any interactions between the three factors of context, hemisphere, and accuracy in LOC (all F < 2.50, all p > .12).

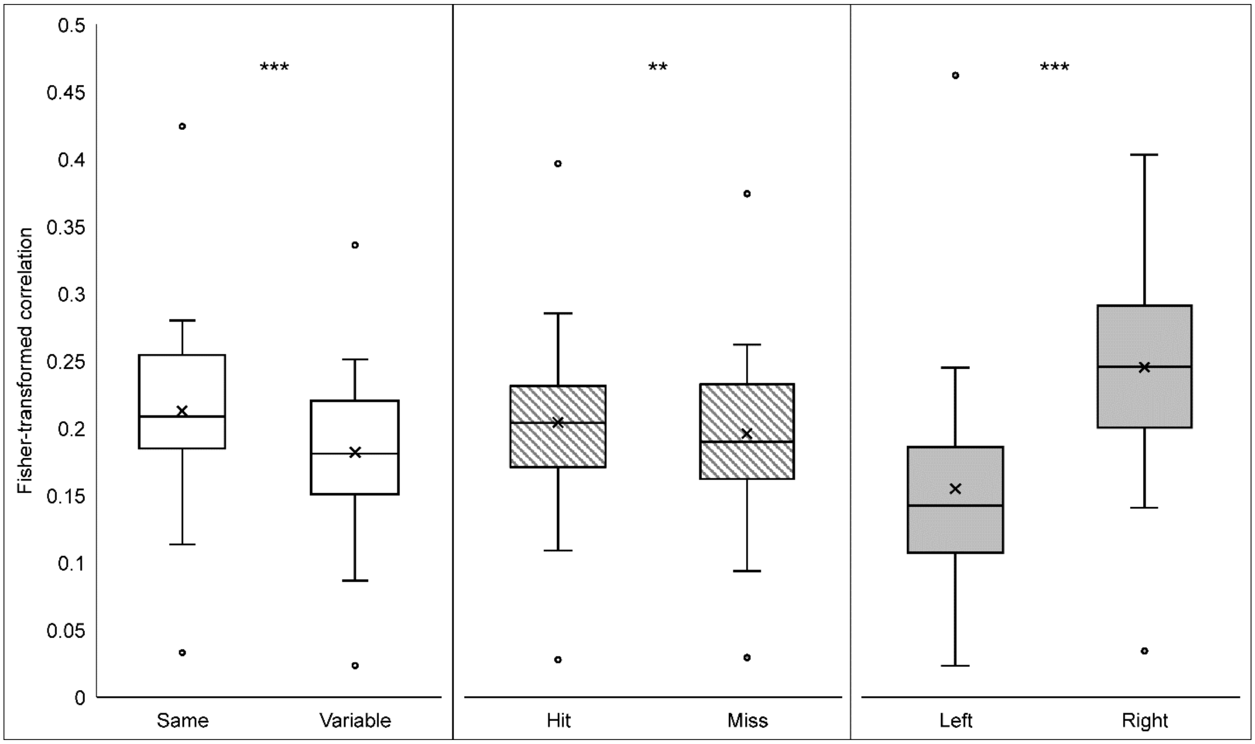

Figure 7. *The distribution of neural pattern similarities, as Fisher-transformed correlations, in LOC for each comparison (Same vs. Variable Context condition, Hit vs. Miss responses, and Left vs. Right hemisphere). "X" indicates the mean value in each collapsed condition, boxes indicate the range of the inner quartiles, whiskers indicate the range of the outer quartiles, and range outliers are plotted as individual points.* *** $p < .001$, ** $p = .004$

3.3.4 Hippocampus

We predicted, based on prior findings in the literature of differentiation between similar events, that decreased hippocampal pattern similarity across repetitions would benefit later item memory regardless of context condition during encoding. We further expected that lower hippocampal pattern similarity would occur for items repeated in the Same Context condition than for those in the Variable Context condition based on prior work showing differentiation in hippocampal representations for similar events (Favila et al., 2016). We did not predict any effects of hemisphere. The results revealed a different pattern of effects in the hippocampus than any other ROI, however the pattern was consistent with our predictions for MTL cortex, rather than for the hippocampus.

The 2x2x2 repeated measures ANOVA conducted on the hippocampal ROI correlations revealed a significant main effect of context ($F(1, 29) = 9.29$, $p = .005$, $\eta_p^2 = 0.24$). Overall, there was a significantly higher hippocampal pattern similarity across the repeated items from the Same Context condition ($M = 0.05$) than the items from the Variable Context condition ($M = 0.04$). This main effect occurred in the opposite direction to our prediction, suggesting that objects studied under more similar contextual conditions did not provoke differentiation as compared to objects studied under more variable contextual conditions. There was no main effect of either memory accuracy ($F(1, 29) = 0.80$, $p = .38$, $\eta_p^2 = 0.03$) or hemisphere ($F(1, 29) = 0.25$, $p = .62$, $\eta_p^2 = 0.01$) in the hippocampus.

The hippocampal ROI revealed a significant interaction between context condition and memory accuracy in pattern similarity, the primary interaction of interest for this study, regardless of hemisphere, ($F(1, 29) = 5.54$, $p = .03$, $\eta_p^2 = 0.16$). Follow-up paired-sample t-tests revealed a significant difference in the Variable Context condition between hits ($M = 0.03$) and misses ($M = 0.04$, $t_{(29)} = 2.88$, $p = .007$; Figure 8), such that hippocampal pattern similarity was **higher** during study of items that would later be **forgotten** than during study of items that would later be remembered. Although the opposite numerical pattern occurred for the Same Context condition, as we predicted for MTL cortex, the difference between the means (hits, $M = 0.05$; misses, $M = 0.04$) was not significant ($t_{(29)} = 1.17$, $p = .25$). The direction of pattern similarity effects, lower for hits than misses, was quite consistent at the individual subject level in the Variable Context condition (Figure 9) but less consistent in the Same Context condition.

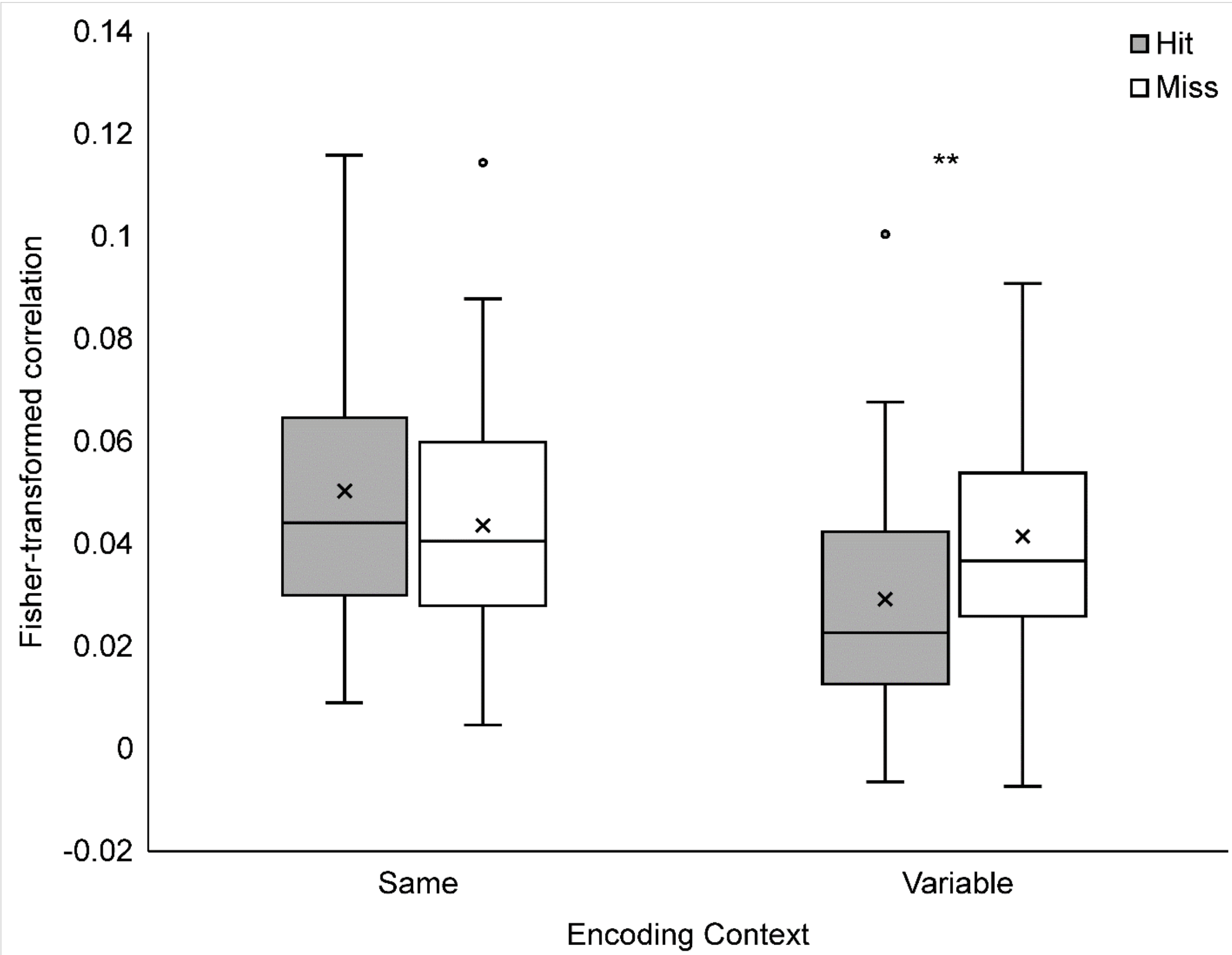

Figure 8. *The distribution of bilateral hippocampal pattern similarity, as Fisher-transformed correlations, for hits and misses in the Same and Variable Context conditions. "X" indicates the mean value in each condition, boxes indicate the range of the inner quartiles, whiskers indicate the range of the outer quartiles, and range outliers are plotted as individual points.* ** $p < .01$

There were no other 2-way interactions in the hippocampal data (both $F < 1.0$, $p > .40$). Finally, there was no significant 3-way interaction between context, accuracy, and hemisphere found in bilateral hippocampus ($F(1, 29) = 0.79$, $p = .38$, $\eta_p^2 = 0.03$).

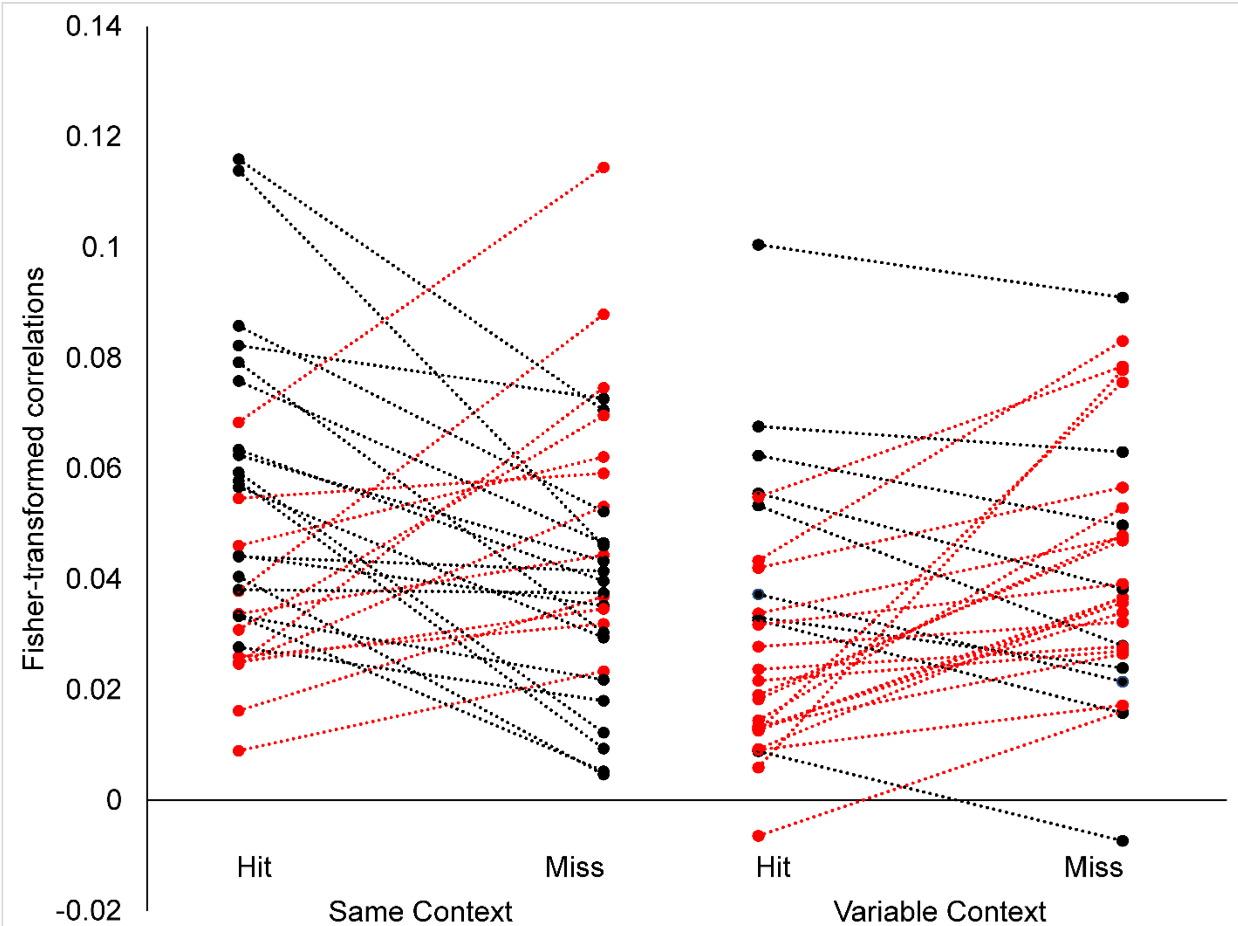

Figure 9. *Individual participant data pairs of hit and miss trials in the Same and Variable Context conditions, which were shown in aggregate in Figure 8. Greater pattern similarity at encoding for subsequent hits as compared to subsequent misses (at the individual participant level) is plotted with black and reduced pattern similarity for hits as compared to misses is plotted with red.*

4.1 Discussion

The current study aimed to discover how pattern similarity across repeated events predicts subsequent memory performance when cognitive goals during encoding were manipulated to be either variable or consistent. We replicated prior behavioral findings from our lab (Salan et al., under review) and others (Sievers, Bird, et al., 2019), that identified a benefit for variable context during encoding in supporting later item recognition. The current study differed from our prior behavioral work in that it implemented a multi-day delay between study and test to reduce overall behavioral performance. The overall reduction in performance as compared to our earlier studies was accompanied by an increase in the performance difference between variable and consistent contexts, indicating that the benefit of variable context encoding for item recognition increases with extended retention.

Although our behavioral findings were consistent with our predictions, the findings in the fMRI pattern similarity analysis were somewhat unexpected. The primary interaction that we predicted, a difference in the relationship between pattern similarity and subsequent memory when items were encoded in variable contexts as opposed to consistent contexts, was found in the hippocampus, rather than MTL cortex. There were no significant interactions between context variability and subsequent memory in the other ROIs we examined.

Instead, MTL cortex (both parahippocampal and perirhinal cortices) and LOC produced significantly larger correlations between the first and second study exposure when the items were studied with the same cognitive goal than when they were studied with different goals, regardless of later memory performance. An interaction between hemisphere and context condition in MTL cortex, but not LOC, revealed that the main effect in MTL cortex effect was driven by the left hemisphere rather than the right. This effect was consistent regardless of whether both right- and left-handed participants or only right-handed participants were included in the analysis. It is possible that the overall larger correlations for items studied in consistent contexts vs. variable contexts were caused by the presence of distinct words on the screen during the first and second study exposure for the Variable Context condition but not for the Same Context condition.

Although these words were not the primary focus of attention, we cannot rule out this influence for any effects that do not compare hits to misses (and therefore only comparing items that always either had the same question on the screen or items that had a different question on the screen). For example, the interaction between hemisphere and context condition in both perirhinal and parahippocampal cortex is consistent with idea that the left hemisphere is more involved in language processing than the right, and that therefore the changing words on the screen between the first and second presentation (as in the Variable Context condition) led to lower left hemisphere correlations for Variable Context items than for Same Context items (for which the words on the screen were identical from the first to second study presentation).

One additional finding unrelated to memory performance is relevant to prior literature. We found that the hippocampus, bilaterally, produced more pattern similarity for items studied with consistent encoding questions than for items studied with variable encoding questions. In other words, the neural patterns in the hippocampus did not show increased differentiation among similar events. The hippocampus has been found to differentiate similar events in at least one prior study (Favila et al., 2016), which conflicts with our findings here. We also note that in our study, the pattern similarity results for Same Context as compared to Variable Context items were consistent across all of our ROIs, with parahippocampal cortex, perirhinal cortex, and LOC showing the same pattern as the hippocampus.

Now turning to the effects that included memory accuracy as a factor, voxel patterns in right MTL cortex, but not left MTL cortex, were sensitive to subsequent recognition success. Increased pattern similarity across repetitions in right parahippocampal cortex and right perirhinal cortex predicted successful memory retrieval after 10 days, regardless of the context manipulation we applied. This effect, higher correlations across two encoding exposures for correctly recognized objects than incorrectly recognized, also occurred in LOC but was not lateralized. These findings are consistent with prior findings in the literature demonstrating that similar neural representations across repeated exposures predict subsequent item memory in various regions of cortex (Feng et al., 2019; Lu et al., 2015; Qu et al., 2017; van den Honert et al., 2016; Ward et al., 2013; Xue et al., 2010). In particular, this effect replicates one prior finding in parahippocampal cortex (van den Honert et al., 2016) and one prior finding in LOC (Ward et al., 2013).

Finally, and most importantly, we did find the predicted interaction between cognitive goals/encoding task and recognition memory accuracy, however the interaction occurred only in the hippocampus and not in the MTL cortex as we expected. In the Variable Context condition, there was significantly reduced pattern similarity in the hippocampus for items that were later remembered than for items that were later forgotten. That is, when the cognitive goal changed from the first to second encoding exposure, a greater distinction in the voxel pattern between those exposures was associated with better memory. The numerical difference between remembered and forgotten items in the Same Context condition (when cognitive goals were consistent from the first to second study exposure) was not statistically significant but was in the opposite direction to the Variable Context condition. Although we did not expect this effect in the hippocampus, based on prior findings in the literature, the interaction between context and accuracy supports our primary theoretical question: that cognitive goals can change the relationship between representational similarity and subsequent memory.

To our knowledge, although this idea was previously raised in a review paper discussing the RSA literature (Brunec et al., 2020), there are not yet any empirical tests of this proposal in the peer-reviewed literature. This finding is critically important for interpreting the fMRI memory literature in that it indicates that cognitive processing must be considered as a relevant factor. We cannot assume that voxel patterns in response to a stimulus are linked purely to that stimulus and its later memorability, but rather must consider that the cognitive goals held by the participant may change the findings. In reviewing the prior literature investigating RSA and memory performance (see Introduction), we found that conclusions about the relationship between pattern similarity during repeated encoding and later memory performance have varied across studies. Our finding of an interaction between cognitive context and the direction of RSA correlation that predicts memory indicates that inconsistencies in the prior literature may be driven by differences in the cognitive tasks of each experiment. This conclusion is of course consistent with decades of research in the cognitive literature, for example the ideas of transfer-appropriate processing (Morris et al., 1977) and encoding specificity (Tulving & Thomson, 1973).

We also note that finding decreased pattern similarity across variable contexts in the hippocampus supporting memory is potentially consistent with the two studies we reviewed above (see section 1.4) that found decreased pattern similarity supporting memory performance in general. Both sets of authors in those studies (Karlsson Wirebring et al., 2015; Veldsman et al., 2017) propose that their findings might be attributed to cognitive differentiation during the repeated study trials. Karlsson Wirebring and colleagues (2015), who found their effects in the right parietal lobe, discussed the role that "encoding variability" may have played in repeated retrieval practice trials with Swedish-Swahili word pairs being learned by Swedish speakers. Veldsman and colleagues (2017), who found their effects in multiple occipital and parietal regions including LOC, discussed the role of semantic elaboration in maintaining recognizable objects in working memory as opposed to unrecognizable objects.

The most similar existing study to the current study, currently only available in non-peer-reviewed forms, both as a dissertation and as a preprint (Sievers, 2018; Sievers, Smith, et al., 2019), reaches very similar conclusions. Sievers and colleagues used a whole-brain searchlight analysis which identified a region in posterior cingulate cortex that showed the same type of interaction between subsequent memory accuracy and contextual manipulation that we found in the current study in the hippocampus. There is some possibility that differences in repetition spacing between the Variable Context condition and the Same Context condition in the Sievers study played a role in their finding. However, given that we controlled spacing in the current study and still found a similar pattern of results we think that is unlikely. Therefore, the primary difference between the two studies is the type of memory accuracy that was examined. Sievers and colleagues did not have sufficient numbers of missed items to analyze pattern similarity as it related to item memory. Their findings showed that varying the cognitive context during encoding resulted in **decreased** pattern similarity across encoding exposures predicting **increased** memory for that cognitive context (source recognition). In contrast, keeping the cognitive context consistent during encoding resulted in **increased** pattern similarity across encoding exposures predicting **increased** memory for that cognitive context. If we infer that thinking about each item differently during variable context encoding will help participants to remember that the item was encoded with variable contexts, the neural findings are very intuitive. The other side of the interaction is also logically intuitive, such that thinking about an item similarly across consistent context encoding will help participants remember that the item was encoded with consistent contexts.

Although our findings occurred for simple item recognition rather than source memory, a similar logic may apply to explain our findings. We did not collect data about the type of recognition processes that contributed to the memory judgments in this task and therefore cannot determine the degree to which participants used recollection (retrieving contextual information) or familiarity (making strength-based judgments) in the task (Yonelinas, 2002). If participants recognized previously studied items by retrieving information about the contexts in which they were studied, we might expect the same pattern to support item recognition as was found to support source recognition in the Sievers study.

The repetition of items during encoding trials raises the possibility that participants were effortfully or spontaneously retrieving the earlier presentation of an item during its second appearance. This phenomenon, sometimes termed “study-phase retrieval” or reactivation, is generally assumed to benefit later memory performance (e.g., Siegel & Kahana, 2014). The Variable Context condition implemented in the current study might decrease the likelihood that reactivation of the first presentation would occur (because the context in which the item is being considered has changed) as compared to the Same Context condition. If so, we would expect pattern similarity to be lower for Variable Context trials than for Same Context trials. Prior studies have interpreted increased similarity in intracranial recordings as an index of reinstatement of an earlier event (Howard et al., 2012). However, it is not clear why the lack of reactivation would predict memory success and therefore this interpretation may not be consistent with our finding that decreased pattern similarity was associated with later recognition in the Variable Context condition.

Another possible interpretation of our key finding speaks to an additional purpose of the current study: to investigate the mechanism by which context variability improves later item memory. Our findings indicate that cognitive context can modify neural representations during encoding but they also suggest that repeated events might be more likely to be encoded in distinct traces when the context is variable than when it is constant (and the events are therefore more similar). Encoding multiple unique traces might provide a better chance to remember the event during retrieval than a single trace would, even if that trace is stronger, thereby explaining the item recognition benefit for the Variable Context condition. Participants may have effortfully reinstated the two given encoding questions to assess whether their resulting responses were familiar. If the items were encoded in variable cognitive contexts, forming unique neural traces in the hippocampus, participants would have two opportunities, one for each encoding question, to successfully retrieve the item. These ideas remain speculative but could be tested in future studies.

5.1 Conclusions

The current study manipulated cognitive goals to determine whether this influences the relationship between neural patterns in response to repeated events and later memory success. Variable cognitive goals during repeated events were beneficial to memory performance. In the hippocampus, representations that were more dissimilar predicted later memory in the variable condition whereas the opposite pattern was seen when the repeated events had unchanging cognitive goals. This finding was unique to the hippocampus and was not seen in MTL cortex or LOC. The results indicate that cognitive goals at encoding affect neural patterns, especially in the hippocampus, and may help to explain inconsistent findings in previous RSA studies of memory.

Acknowledgements

This work was supported by the National Science Foundation [grant number 1850674]. The sponsor was not involved in study design, data collection/analysis, writing the report, or deciding to submit the article for publication. We thank Jefferson Salan, Eleni Tsiamis, Marali Harikar, Mohammed Zerouk, Rebekah Schlitzer, and Madisenn Smith for assistance with data collection. Declarations of interest: none

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