THE INFLUENCE OF VALID AND INVALID CONTEXT MEMORY CUES AT ENCODING

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LIST OF SYMBOLS AND ABBREVIATIONS

EEG	Electroencephalography
fMRI	Functional Magnetic Resonance Imaging
SME	Subsequent Memory Effects
MVPA	Multivariate Pattern Analysis

SUMMARY

This dissertation investigated how preparation influences episodic memory encoding. Previous neuroimaging research has shown that the time period before encoding new information is sensitive to the success of later retrieving that information (for review: Cohen et al., 2015; Otten, Quayle, Akram, Ditewig, & Rugg, 2006). The manifestation of these preparatory processes is sensitive to task characteristics, such as stimulus type (Otten et al., 2006) and task type (Padovani, Koenig, Brandeis, & Perrig, 2011). They can also be strategically utilized, or not, in response to these demands, such as valuation (Gruber & Otten, 2010), instructions (Schneider & Rose, 2016), and difficulty (Park & Rugg, 2010). These preparatory processes may reflect an optimal state in which the brain is ready to encode new information (Addante, de Chastelaine, & Rugg, 2015; Galli, Bauch, & Gruber, 2011). This optimal state is likely task dependent such that both patterns of high and low activation within task relevant regions may facilitate encoding (Yoo et al., 2012). The current literature has largely revolved around how changes in task characteristics influence the prestimulus neural correlates of successful encoding. While it is clear that the time period before a to-be-encoded item may reflect the success of later retrieving that item, it is unclear if this is epiphenomenal or if the preparatory processes direct contribute to encoding success.

In non-memory studies of preparatory attention, informative prestimulus cues recruit task relevant cognitive processes in expectation of the upcoming stimulus. These studies generally find that the utility of preparation is related to the validity of the information used for preparation (Petersen & Posner, 2012; Posner & Petersen, 1990), such

that accurate cues enhance performance while inaccurate cues impair it. One limitation with the current episodic memory literature is that all the cues are valid. The encoding cues all provide accurate information about the specific trial, which confounds the effect of preparation with differences in trial type.

To assess the influence of preparation on successful encoding, as opposed to previous studies that looked for task related changes in preparation, I needed to control for strategic and stimulus differences between our preparatory conditions. In-order to do this, the validity of preparation at encoding was manipulated by cuing participants to a specific trial context and either keeping it (valid) or changing it (invalid) when the to-be-encoded item was presented. For each encoding trial, the participant made a judgement about the likely pairing of an item image and one of the four scene images. Each trial was preceded by a descriptive label cue indicating one of the context scenes or a non-descriptive cue. For invalid trials, the cued scene did not match the scene used in the item-scene judgement. A neutral condition was included to provide a behavioral comparison point for context memory without informative preparation. To encourage the adaptation of attending and using the cue information, a required cue condition was included. For required cue trials, a scene was not provided during stimulus presentation and the likelihood judgment was based on the cued scene. Since the participant was unaware if the cue was valid or invalid, there should not be any intrinsic strategic differences between the two conditions during the cue -stimulus interval. Before the encoding task, a familiarization task was used to associate the four scene labels with the four specific scene images. At retrieval, each item from encoding plus additional new items were presented one at a time and the participant had to select which scene the item was paired with or indicate the item was not presented

during encoding (new). After the context (i.e. scene) memory judgement, participants indicated their confidence in the response. To assess the neural correlates of successful encoding and preparation, electroencephalography (EEG) was recorded for each participant across all tasks in the session. I investigated three frequency bands within the EEG (theta, alpha, and beta) to assess pre and post-stimulus neural differences in context memory performance. Multivariate pattern analyses (MVPA) where used to assess if participants were reactivating the scene image in response to the cues, and if the post-stimulus neural patterns were influenced by the invalid cue.

I hypothesized that using the cued scene to prepare would facilitate encoding on trials with a valid cue and interfere on trials with an invalid cue. I found that interfering with the expected context selectively impaired context memory performance and not item memory. Patterns of preparatory neural activity within the alpha frequency band was found to positively relate to valid context memory performance, and negatively relate to invalid context memory. In addition, alpha desynchronization correlated with greater context memory in valid trials only. In further support of the invalid cue interfering with processing the item-scene pairing, discriminable scene patterns of neural activity in the post-stimulus time period were only reliable for trials with a valid cue. Univariate analyses suggest invalid trials required greater encoding demands, as reflected by greater beta desynchronization. At retrieval, less theta synchronization and greater alpha desynchronization correlated with higher context memory performance for trials in the invalid encoding cue condition, suggesting that participants who failed to resolve the invalid cue interference at encoding had worse context memory performance.

In sum, this dissertation provides a novel task paradigm for investigating preparatory effects that controls for both stimulus and task characteristics. This brings together both the episodic memory literature and the attentional cuing literature in order to further understand the role of attention in successful episodic memory encoding. The results add to the current understanding of preparation during episodic memory encoding by finding conjoining evidence across behavioral, univariate, and multivariate analyses of neural oscillations that the utility of preparation during encoding is related to the accuracy of the prepared content.

CHAPTER 1. INTRODUCTION

Episodic memory is the memory for specific events or experiences that are rich in contextual details, such as the location, time, and other coexisting elements (Tulving, Donaldson, & Bower, 1972). These elements are represented in the cortex as perceptual and cognitive processes, and a memory representation is comprised of those processes that are active during the event or experience (for review: Craik, 2002). While abundant research has focused on the neural activity that occurs after the event (for review: Paller & Wagner, 2002), recent evidence has shown the activity preceding a to-be-encoded event also reflects subsequent memory performance (for review: Cohen et al., 2015; Otten et al., 2006), suggesting the cognitive processes engaged prior to encoding are part of the resulting memory representation. When the event is later remembered, the processes active during encoding are thought to be reengaged (Damasio, 1989; Norman & O'Reilly, 2003; Rugg, Johnson, Park, & Uncapher, 2008). Studies of reactivation have found reengagement of sensory regions (Wheeler, Petersen, & Buckner, 2000) and reinstatement of neural patterns from encoding at retrieval (Johnson, McDuff, Rugg, & Norman, 2009; Polyn, Natu, Cohen, & Norman, 2005).

Numerous studies on preparatory attention (e.g. spatial, perceptual) have suggested the accurate preparation of task-relevant demands improves performance, while inaccurate preparation impairs performance (Luck, Woodman, & Vogel, 2000; Petersen & Posner, 2012). Accurate and inaccurate preparation can be manipulated with valid and invalid prestimulus cues, respectively. An example of inaccurate (i.e. invalid) preparation would be expecting a stimulus to show up on the right side of the screen when it shows up on the

left. Conversely, accurate (i.e. valid) preparation would be expecting a stimulus to show up on the right side of the screen when it shows up on the right. Changes in performance are thought to be driven by anticipatory neural activity that biases expectation for a specific task element over other task elements (for review: Petersen & Posner, 2012; Posner & Petersen, 1990). For example, spatial cuing paradigms find valid location cues are elicit faster responses than invalid location cues, which is accompanied by lateralized shifts in neural activity (for review: Luck et al., 2000). Expectation-driven neural activity has also been found during category (Puri, Wojciulik, & Ranganath, 2009) and task (Luks, Simpson, Dale, & Hough, 2007) preparation. The utility of accurately preparing for an expected stimulus in terms of spatial (e.g. 'Is it a left or right highway exit?') or perceptual (e.g. 'Is that a bear or a bush?') tasks is quite clear. However, the role of expectation in episodic memory encoding is less established.

The circumstances under which preparatory processes benefit versus impair memory performance are still unknown. For example, does an inaccurate expectation during encoding interfere with successful encoding, and does an accurate expectation facilitate successful encoding? The current dissertation investigated the effect of accurate and inaccurate expectation on learning item-scene associations to test if the validity of the expectation directly relates to successful memory performance.

1.1 Long-term Memory Encoding and Retrieval

The subsequent memory paradigm is commonly used to investigate the neural correlates of successful encoding, where neural activity for remembered items are contrasted with forgotten items (Paller, Kutas, & Mayes, 1987; for review: Paller &

Wagner, 2002). Both functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) show robust subsequent memory effects (SME). A meta-analysis of fMRI studies assessing SMEs during encoding of verbal (e.g. words) and pictorial material found common and material-specific effects. Common effects were found across bilateral hippocampus, fusiform cortex, premotor cortex, posterior parietal cortex, and the left inferior frontal cortex. The fusiform cortex and hippocampus were more engaged during pictorial than verbal material, whereas the left inferior frontal cortex was more engaged for verbal material (Kim, 2011). In addition to stimulus properties, subsequent memory effects are also found to differentiate between orienting tasks at encoding. For example, semantic (i.e. animacy) tasks are more likely to recruit regions in the left prefrontal cortex, while phonologic (i.e. syllable) tasks recruit additional right prefrontal regions, left occipital gyrus, bilateral fusiform gyrus, and bilateral intraparietal sulcus (Otten & Rugg, 2001b). EEG studies have also found temporal and topographical SMEs related to specific task and stimulus properties for event-related potentials (Jordan, Kotchoubey, Grozinger, & Westphal, 1995; Otten & Rugg, 2001a; Paller et al., 1987) and neural oscillations (Fellner, Bauml, & Hanslmayr, 2013; Hanslmayr, Spitzer, & Bauml, 2009; Hanslmayr & Staudigl, 2014; Khader & Rösler, 2011; Klimesch, 1999; Staudigl & Hanslmayr, 2013; Waldhauser, Johansson, & Hanslmayr, 2012). The specific manifestation of SMEs are a function of successfully processing the to-be-encoded item with the coexisting perceptual or cognitive processes (i.e. encoding context) to create a detailed memory representation. When retrieving the information, the subsequent neural representation is thought to be a mixture of reengaging the associated cognitive and

perceptual processes and the retrieval criteria (Johnson & Rugg, 2007; Khader & Rösler, 2011; Wagner et al., 1998; Wheeler et al., 2000; Wheeler et al., 2006).

The neural processes utilized at encoding are thought to be reengaged during the retrieval experience (Damasio, 1989; McClelland, McNaughton, & O'reilly, 1995; Rugg et al., 2008). For example, recall of visual or auditory information has been shown in fMRI studies to reactivate the respective sensory regions (Wheeler et al., 2000). Similarly, in an EEG study where items were encoded with a stimulus flicker at 6 or 10 Hz the researchers found reactivation of the respective frequency bands during item retrieval (Wimber, Maass, Staudigl, Richardson-Klavehn, & Hanslmayr, 2012). Multivariate pattern analyses, which use patterns of activity across data points (e.g. voxels, electrodes, sensors) to make inferences about the representational content reflected in the neural data (Norman, Polyn, Detre, & Haxby, 2006), also support a reactivation hypothesis (for review: Jafarpour, Horner, Fuentemilla, Penny, & Duzel, 2013; Kuhl, Rissman, & Wagner, 2012; Morton et al., 2012). Supporting the role of the hippocampus in long-term memory (Bliss & Collingridge, 1993) these representations are thought to be reactivated via connections between the hippocampus and the cortex (Norman & O'Reilly, 2003).

1.2 Preparatory Cuing in Memory

Abundant research has implicated the time period before a to-be-encoded event as part of the encoding process (for review: Cohen et al., 2015; Otten et al., 2006). These prestimulus processes are found to be sensitive to task characteristics, such as encoding task (Galli, Choy, & Otten, 2012; Padovani et al., 2011), task switching (Padovani, Koenig, Eckstein, & Perrig, 2013), type of stimulus (Addante et al., 2015; Mackiewicz,

Sarinopoulos, Cleven, & Nitschke, 2006; Otten et al., 2006; Otten, Quayle, & Puvaneswaran, 2010; Park & Rugg, 2010), available processing resources (Galli, Gebert, & Otten, 2013), gender of participant (Galli, Griffiths, & Otten, 2014), and item value (e.g. reward for remembering) (Gruber & Otten, 2010). In addition, these processes are susceptible to instructional differences (Schneider & Rose, 2016) and likely under some form of voluntary control (Gruber & Otten, 2010), suggesting that similar studies may find differing results due to uncontrolled confounds. For example, in two EEG memory studies with informative cues (indicating modality type) preceding audio and visual items, one found effects immediately prior to stimulus onset (Otten et al., 2006) while the other found longer sustained effects reaching significance in the middle of the cue-stimulus interval (Otten et al., 2010).

Another possibility for the large amount of variability in prestimulus effects may be due to the necessity of the cue. Informative prestimulus cues in some studies are required to perform the encoding task (Otten et al., 2006; Padovani et al., 2011); in others, the cues, while informative, are not required (Addante et al., 2015; Galli et al., 2012; Galli et al., 2014; Mackiewicz et al., 2006; Otten et al., 2010; Park & Rugg, 2010). Having an unrequired cue could increase the amount of variability across participants in how the cues are utilized. For example, an individual could ignore it, shift attention (e.g. inhibit irrelevant thoughts, bias relevant processing regions), retrieve a related or previous item, or do something else completely. In two imaging studies that used a very similar design consisting of visual and auditory words with an informative but unrequired cue, which indicated the upcoming presentation modality, differences were found in both the behavioral and imaging data. In the EEG study, equivalent performance and imaging

results were found between the modalities (Otten et al., 2010). In the fMRI study, memory performance for visual items was greater than auditory items, and audio items showed additional prestimulus activity not found for visual items (Park & Rugg, 2010). These two studies highlight that the role and use of preparatory processes are susceptible to across study differences in participant samples. Given the variability across participants in utilizing prestimulus cues, the utility of the cues is difficult to interpret.

When the cues are required, such as when they indicate the encoding task to perform, SMEs could reflect the advanced engagement of task-relevant processes to facilitate performance. Another possibility is that on those trials with prestimulus task-relevant engagement, the participant has a greater probability of attending to the upcoming stimulus, which could lead to a higher probability of those trials being remembered. While an attention-only hypothesis is unlikely given the task-related findings, task preparation and attention could interact. In an EEG study that investigated incidental vs intentional encoding of pictures with animacy judgements, only the intentional group was found to have prestimulus SMEs (Schneider & Rose, 2016). Given that both groups had equivalent memory performance, this suggests that the intention to learn only changed how participants approached the items (Schneider & Rose, 2016). In addition, memory studies that use informative prestimulus cues confound cue type with trial type, making it difficult to separate trial-specific preparation from other trial characteristics. In sum, preparatory processes are influenced by task type, stimulus type, individual differences, instructions, necessity of cue, task difficulty, and the interactions between these factors. The large amount of variability suggests that the neural context preceding a to-be-encoded event is

included in the resulting memory representation, but the utility of the preceding neural context is still an open question.

Many of the studies previously discussed have suggested the preparatory engagement of task-specific processes contribute to successful memory encoding, as reflected by increased prestimulus neural activity, though it is currently unclear if preparatory processes are beneficial to memory performance. Brain-behavior correlations with fMRI have found both positive (Mackiewicz et al., 2006) and negative (Addante et al., 2015) relationships between the hippocampus and memory performance. In the parahippocampal place area, prestimulus activity has been shown to positively correlate with the successful encoding of scenes (Turk-Browne, Yi, & Chun, 2006), while real-time fMRI has shown that less activity in the parahippocampal place area immediately prior to scene presentation increases the likelihood of successfully encoding an upcoming scene (Yoo et al., 2012). Therefore, it is still an open question whether these effects reflect processes that facilitate, interfere, or act in some combination to influence subsequent memory performance.

1.3 Neural Oscillations

Neural oscillations are an excellent tool for investigating the correlates of cognition and memory, as they are thought to reflect the communication patterns of neurons. Oscillatory activity within the EEG have been shown to reflect the synchronized inhibitory and excitatory pattern of neural firing rates (Jacobs, Kahana, Ekstrom, & Fried, 2007), which is thought to underlie flexible communication within and across cortical regions(Fries, 2005). An oscillatory signal for a frequency is comprised of both power and

phase. Phase refers to the location within the oscillatory cycle, while power refers to the collective amount of post-synaptic potentials firing independent of phase. In separating power and phase, oscillatory activity allows for the investigation of cognitive processes that have trial by trial variability (e.g. maintenance, post-retrieval processing). ERPs are dominated by the lower frequencies (under 20 Hz), and only reflect phase locked activity (i.e. cognitive processes with low trial by trial variability) (Cohen, 2014). One consequence of using oscillations is a reduction from the temporal resolution found in ERPs. Despite this, oscillations provide a greater representation of the underlying communication networks engaged during cognition than ERPs, while maintaining better temporal resolution than fMRI.

Oscillations are commonly parsed in functionally separable frequencies bands that correspond to: Delta (~1 - 4 Hz), Theta (~4 - 7 Hz), Alpha (~8 - 12 Hz), Beta (~12 – 30 Hz), and Gamma (~30+ Hz) (for review: Klimesch, 1999; Klimesch, 2012; Klimesch, Doppelmayr, Pachinger, & Ripper, 1997). Changes in power, commonly referred to as synchronization or desynchronization, reflect a relative increase or decrease in the number of neurons oscillating within a frequency band from a prestimulus baseline, respectively (Pfurtscheller, 1977). In long-term memory studies, the prevalent pattern of results for SMEs consist of greater synchronization (increases) in theta power, and greater desynchronization (decreases) in alpha and beta power at both encoding and retrieval (for review: Klimesch, 1999; Osipova et al., 2006; Zion-Golumbic, Kutas, & Bentin, 2010), although opposite patterns are also found (for reviews: Hanslmayr & Staudigl, 2014; Hanslmayr, Staudigl, & Fellner, 2012).

The process of binding together an item with a context is thought to rely on communication between the hippocampus and prefrontal cortex, via theta oscillations (for review: Hanslmayr & Staudigl, 2014; Sirota et al., 2008). For example, theta SMEs during encoding have been localized to medial temporal regions in both MEG (Guderian, Schott, Richardson-Klavehn, & Duzel, 2009) and combined EEG-fMRI (Hanslmayr et al., 2011) studies. Intercranial EEG also supports the role of frontal-temporal theta during successful encoding (Sederberg, Kahana, Howard, Donner, & Madsen, 2003). Memory related theta power is consistently found during the successful recovery of contextual details and is thought to reflect the associative links between an item and the contextual elements (Fellner et al., 2013; Hanslmayr & Staudigl, 2014; Jacobs, Hwang, Curran, & Kahana, 2006; Staudigl & Hanslmayr, 2013; Strunk, James, Arndt, & Duarte, 2017). Theta power has been shown to parametrically modulate with the number of items during working memory maintenance (Jensen & Tesche, 2002) and the number of contextual features during retrieval, without differentiating between contextual features (e.g. location, stimulus) (Khader & Rösler, 2011). Prestimulus encoding related theta may reflect the activation (or retrieval) of contextual elements (e.g. task, stimulus modality) that influences the processing of an upcoming stimulus (Fell et al., 2011; Guderian et al., 2009). During retrieval, both prestimulus and post-stimulus theta power have been shown to be positively correlated with memory performance and with each other (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011). Overall, memory related theta oscillations are believed to reflect the working memory processes that create the associative links between an item and its contextual elements as well as the reactivation of those associations during retrieval (for review: Hanslmayr & Staudigl, 2014).

Alpha and beta oscillations are also found in memory studies during both encoding and retrieval, with the typical pattern of greater decreases for subsequently remembered trials (for reviews: Klimesch, 1999, 2012; Klimesch, Sauseng, & Hanslmayr, 2007). Alpha is closely related to attention and thought to control the flow of information within the cortex through inhibition (for reviews: Hanslmayr & Staudigl, 2014; Klimesch et al., 2007) and thus, plays an important role in suppression and selection of task relevant regions (Jokisch & Jensen, 2007; for review: Klimesch, 2012). Alpha desynchronization is commonly linked to improved performance, but under some conditions alpha synchronization is also reflective of improved performance. For example, when items need to be maintained across an interval, alpha synchronization may protect the contents of working memory from interference (Meeuwissen, Takashima, Fernandez, & Jensen, 2011), or when competing information needs to be isolated or inhibited (Waldhauser et al., 2012). During context memory retrieval, alpha and beta activity have been shown to modulate with quantity of retrieved information and discriminate between the types of information retrieved (Khader & Rösler, 2011). Which suggests that alpha and beta are involved with reconstructive processes during retrieval. In a combined EEG-fMRI study, beta, but not alpha, desynchronization was localized to the left inferior prefrontal gyrus during semantic processing, and subsequent memory performance (Hanslmayr et al., 2011). The role of beta in subsequent memory is less clear, as it commonly shows up with similar patterns of activity as alpha. This could be due to individual differences in frequency band limits (for review: Klimesch, 1999), similar top-down inhibitory functions that operate at different distances across the cortex, or that beta is signaling the status or maintenance of a cognitive process (Engel & Fries, 2010). During retrieval, beta band activity may be related to the

successes of post-retrieval processes (Strunk et al., 2017). While at encoding, the beta band could reflect a general memory promoting state (Salari & Rose, 2016). Both these processes may operate through a similar desynchronization mechanism that is consistently found within the alpha frequency band (for review: Hanslmayr et al., 2012). Thus, alpha and beta are likely to reflect the ongoing cognitive and perceptual processing demands during both encoding and retrieval.

To summarize, in long-term memory tasks, spatial and temporal patterns of neural oscillations within the theta band are reflective of successfully binding together associations between elements of a to-be-encoded event, and within the alpha/beta bands are reflective of the cognitive and perceptual processes engaged in response to the specific details of those associations. The current dissertation focused on the theta, alpha, and beta frequency bands.

1.4 Multivariate Pattern Analyses

Multivariate pattern analyses (MVPA) utilizes patterns of neural data that may be lost with conventional methods. Conventional methods increase the signal to noise relationship by averaging over data points, at the expense of losing weak or fine grain patterns that could discriminate between conditions of interest. Instead of averaging across data points to increase sensitivity, MVPA uses the coactivating patterns to increase sensitivity. In other words, conventional methods provide a measure of activity, while MVPA can make inferences about the representational content (Norman et al., 2006). Previous research has shown that across image category (e.g. scenes, objects, faces) classification is reliable in both fMRI and EEG (Chan, Applegate, Morton, Polyn, &

Norman, 2013; Manning, Polyn, Baltuch, Litt, & Kahana, 2011; Morton et al., 2012; Polyn et al., 2005), and within category (e.g. scenes) discrimination has been shown in fMRI (Johnson & Johnson, 2014). In addition to visual scene classification, MVPA has been successfully used to decode various cognitive processes, such as the contents of short-term memory (LaRocque, Lewis-Peacock, Drysdale, Oberauer, & Postle, 2013), tracking semantic organization across time (Morton & Polyn, 2017), and predicting subsequent memory performance for an item (Kuhl et al., 2012; Morton et al., 2012).

Typically, MVPA analyses are run within a participant and quantify how dis/similar the conditions of interest are by the ability to accurately discriminate between them. This is commonly done by dividing a dataset into two groups, the training dataset and the test dataset. The training dataset is used to create a classifier that represents the discrimination limit between the conditions. Then, the classifier is applied to the test dataset, and performance is measured by the classifier's ability to correctly distribute the trials in the test data (for review: Norman et al., 2006). For the test dataset, the classifier estimates the amount of evidence for each condition on each trial and selects the condition that has the most evidence, for a measure of overall performance. In addition to overall classifier performance, the amount of evidence for each condition can be tracked and has been shown to increase with subsequent within category representation (Chan et al., 2013; Morton et al., 2012; Morton & Polyn, 2017). Thus, MVPA provides a powerful tool for understanding the representational content during the expectation period.

1.5 Current Study

Given the variability in prestimulus SMEs, the current dissertation aimed to investigate the relationship between task related preparation and memory performance, without stimulus or orienting task confounds. For each trial, the validity of expectation was manipulated with a prestimulus cue by using valid, invalid, neutral, or required prestimulus context cues during an item-scene association task. Before encoding, a familiarization task paired four context images with descriptive labels (i.e. “city”, “forest”, “home”, “office”). During encoding, one of the descriptive labels or a non-descriptive neutral label (“-----”) served as the prestimulus cue for each trial. For valid cues, the prestimulus cue was predictive of the scene used in the item-scene association task. For invalid cues, the prestimulus cue did not match the scene in the item-scene association task. For neutral cues, the prestimulus cue was not contextually informative for the item-scene association task. For required cues, a scene was not provided during the item-scene association task and the judgement was based on the prestimulus cue. Required-cue trials were included to reinforce the necessity of using the cue. The four cue conditions were randomized across trials. At retrieval, all old items were presented, and participants indicated which of the four scenes was used to make the judgement with the item during encoding. Before the encoding task, a familiarization task was used to facilitate associations between the label cues and the four specific scene stimuli, as well as provide a training dataset for the MVPA. EEG was recorded across the whole session and used to assess differences in neural activity to successful and unsuccessful context memory.

As previously discussed, I hypothesized that preparation influences successful encoding. Specifically, if the cue reactivates the associated scene then valid cueing would facilitate context memory (i.e. scene) encoding while invalid cueing would interfere with

it. For the invalid condition this could be considered retrieval induced interference. Since the target of interference was the scene, I did not predict differences in item memory.

Behaviorally, I predicted that context memory would be greater for valid compared to invalid trials. Reaction times are not commonly assessed in episodic memory tasks but are during attentional orienting tasks (for reviews: Petersen & Posner, 2012; Posner, 1980). Thus, reaction times were assessed, and in line with the previous research I predicted that reaction times for valid trials would be faster than invalid trials.

During the preparatory period at encoding I predicted that the scene would be retrieved in response to the cue. During successful retrieval, both theta synchronization and alpha / beta desynchronization are commonly found (Klimesch, 1999). For the valid condition, I predicted that preemptively retrieving the scene image would benefit performance, and thus the neural manifestation of retrieval should be positively related to context memory performance. For the invalid condition, I predicted that retrieval induced interference would reduce performance, and thus the neural manifestation of retrieving the cued image should be negatively related to context memory performance. Specifically, I expected that greater theta synchronization, and greater alpha / beta desynchronization would reflect successful context memory encoding for valid trials. For invalid trials I expected the opposite, less theta synchronization and less alpha / beta desynchronization, would reflect successful context memory encoding.

MVPA was used to assess the representational content during the preparatory period at encoding. If participants are retrieving the cued scene, then MVPA should be able to successfully discriminate between the reactivation of the four cued scenes. Under the

hypothesis that cue validity modulates the influence of the retrieved cued scene, I predicted that greater evidence of reactivation to the scene cues would correlate positively with valid context memory, and negatively with invalid context memory.

During the post-stimulus period of encoding I expected greater demands on invalid trials compared to valid trials. As discussed previously, theta synchronization and alpha desynchronization have been shown to modulate with the amount of information held in working memory (Jensen & Tesche, 2002) and retrieved from long-term memory (Khader & Rösler, 2011). In addition, beta desynchronization has been linked to the violation of expectation, the interruption of an active cognitive process (Engel & Fries, 2010), and top-down prediction errors (Arnal, Wyart, & Giraud, 2011). Given the additional interfering scene associated with the invalid trials, I predicted greater theta synchronization and greater alpha / beta desynchronization. In addition, if the invalid cued scene is maintained into the presentation period then the neural pattern during the post-stimulus period should contain elements of both the cued and the presented scenes. I predicted higher classification accuracy for the valid trial scenes than the invalid trial scenes.

During retrieval of the item-scene pairings for valid trials I predicted greater theta synchronization and greater alpha / beta desynchronization as these have been associated with the retrieval of contextual information and post retrieval processing, respectively. For the invalid condition, I predicted three possible outcomes. The first possibility was that the neural patterns look like valid trials, which would suggest that any interference caused by the invalid cue was resolved during encoding. The second possibility was that I would find greater theta synchronization and greater alpha / beta desynchronization for successful context retrieval, which would suggest the retrieval of both cued and presented scenes and

the greater post retrieval demands required to evaluate both options. The third possibility was that I would find less theta synchronization and less alpha / beta desynchronization for successful context retrieval, which would suggest that correct trials are less likely to have the invalid cue scene associated with them and subsequently less interference during retrieval.

CHAPTER 2. METHOD

2.1 Participants

Twenty-five young adult participants (19 Female) aged 19 to 34 (Mean: 24, SD: 4.34) with an average of 15.84 (SD = 1.89) years of education were recruited from Georgia Institute of Technology and the surrounding community. All participants were native English speakers, had normal or corrected vision, right handed, generally healthy, free of any diagnosed neurological disorders, and not taking any psychoactive medications or central nervous systems stimulants. Participants earned either 1 hour of class credit or $15 for each hour of participation. All participants signed consent forms approved by the Georgia Institute of Technology Institutional Review Board.

2.2 Materials

All 420 color item images and four context scenes were collected from visual object databases (Brady, Konkle, Alvarez, & Oliva, 2008; Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010) and Google images. All item images were downsized to 192 x 192 pixels. The four scene images, seen in Figure 1, of a forest, city, office, and house were collected from Google images and downsized to 550 x 550 pixels. All text was presented in white Helvetica font at a size of 36. All tasks were presented on a black background screen. Participants were positioned two feet from the screen.

Figure 1: The 4 scene images used for context memory

2.3 Procedure

Each participant came in for a single session, lasting approximately three and a half hours. Each session started with the participant filling out a consent form and lab paperwork, followed by applying the EEG electrodes. Next the participant completed three minutes of eyes open and three minutes of eyes closed EEG, followed by the familiarization task, then the encoding task, and finally the retrieval task. Before each task, instructions were given via a written document and fully explained, then the participant completed a short practice block, and finally they were questioned for understanding the task instructions. Participants were not told about the retrieval task until after the encoding task. Two questionnaires about the participants experience were filled out during the session, the first was completed after encoding, and the second was done after retrieval. At the end of the session, participants were debriefed and paid for their participation. The familiarization, encoding, and retrieval task were partially self-paced with minimum and maximum response times.

2.3.1 Familiarization Task

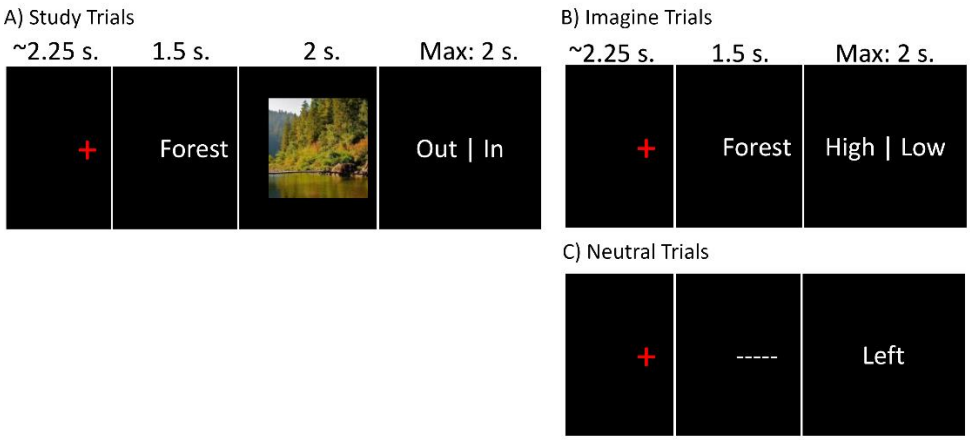

Figure 2: Familiarization Task. A) Study Trials: The first 45 trials of each block (9 presentations of each scene and neutral trial). B) Imagine Trials: The last 10 trials of each block (2 presentations of each scene and neutral trial). C) Neutral Trial: Intermixed between study (9 presentations per block) and imagine (2 presentations per block) phases and uses the same timing as the Imagine Trials.

The familiarization task as seen in Figure 2, serves two functions. The first function is to create an overlearned representation of the four scene images and their respective labels. The second function is to serve as the training dataset for the MVPA analysis, to be tested on the encoding task. Across the whole familiarization task, each scene and neutral label was presented 45 times during the study phases, and 10 times during the imagine phases. These were even distributed across 5 blocks, with each block starting with the study phase and concluding with the imagine phase. For each cue type (scene or neutral) each block contained 9 presentations randomly distributed during the study phase and 2 presentations randomly distributed during the imagine phase. Each block took ~6 mins with a total task time of ~30 mins (Mean = 30.12 mins; SD = 2.83 mins). Trial randomization was constrained so that each trial used a different cue than the previous trial.

For the scene study trials, each trial began with a jittered inter-trial interval of approximately 2.25 seconds (+/- 0.25 seconds), followed by a 1.5 second cue presentation,

and then a 2 second scene presentation. After the scene presentation the participant indicated the scene category ("Outside | Inside"), with the right index and middle fingers. If the participant did not respond within 2 seconds, the next trial began. These trials were used as the MVPA training set for assessing reactivation of the four scene cues during encoding.

For the scene imagine trials, each trial began with a jittered inter-trial interval of approximately 2.25 seconds (+/- 0.25 seconds), followed by a 1.5 second cue presentation. After the cue presentation the participant was instructed to imagine the scene and rate the quality or vividness of their representation ("High | Low"), with the right index and middle fingers on the 1 and 2 keys of a number pad. If the participant did not respond within 2 seconds, the next trial began. These trials were used to necessitate a clear representation of the scene when cued, as well as a MVPA testing dataset to assess reactivation on trials where the participant was explicitly cued to imagine a specific scene.

For the neutral trials, each trial began with a jittered inter-trial interval of approximately 2.25 seconds (+/- 0.25 seconds), followed by a 1.5 second cue ("-----") presentation. After the cue presentation the participant was instructed to respond with either the right ("Right") or left ("Left") response key, with the right index and middle fingers. If the participant did not respond within 2 seconds, the next trial began.

Participants were instructed as follows: "The following task has five blocks, and each block has two trial types (study followed by imagine trials). You will respond with the '1' and '2' keys. On the study trials, one of 4 scenes will be randomly presented and preceded with a cue label. Please study this image and its associated label. After the scene

is presented, a response prompt will appear asking you to indicate if the scene was indoor or outdoor ("Out| In"). Please do so with the index and middle finger of your right hand on the response pad. On imagine trials, you will only be shown the label (e.g. "Forest"), please create a mental image of the associated scene. After the cue label is presented, the response prompt will ask you to indicate how vivid your mental image is ("High | Low"). Throughout both the study and the imagine trials, neutral trials without a scene and a nonword cue label ("-----") will randomly appear. After the neutral label, a response prompt will appear that will indicate which button to press ("Right" or "Left"). We will now complete a short practice. The task is not self-paced, please only respond once per trial. Do you have any questions?" If the participant did not understand the task, instructions and practice were repeated until they did.

2.3.2 Encoding Task

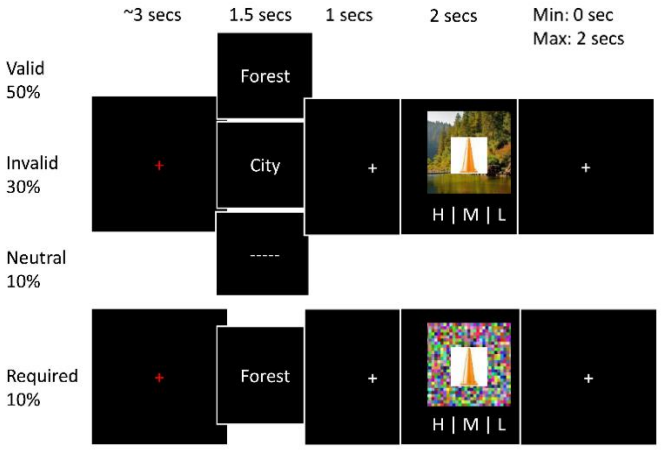

Figure 3: Encoding Task

As shown in Figure 3, the encoding task consisted of four trial conditions: Valid (VAL), Invalid (INV), Required (REQ), and Neutral (NEU). In total 400 encoding trials

were distributed as: Valid (50%, 200 trials), Invalid (30%, 120 trials), Neutral (10%, 40 trials), and Required (10%, 40 trials). This distribution was kept consistent across the eight blocks with 50 trials in each block. Each trial was partially self-paced such that each block took between 6.25 and 8 mins, for a total task time between 50 and 64 mins (Mean = 55.92 mins; SD = 4.52 mins). Each condition was pseudo-randomized within each block, so that each condition did not occur more than three times in a row. For each trial, participants made a likelihood judgement ("High", 'Medium", "Low") about finding the item in the associated scene. For valid, invalid, and neutral trials the item was superimposed on associated scene. For required trials, the item was superimposed on a random color patchwork and the item-scene judgement was based on the cued scene. Participants responded with the index, middle, and ringer fingers of the right hand on the 1, 2, and 3 keys of a number pad. Items were overlaid on the scenes and presented centrally to control for potential lateralization effects in the EEG. After completion, a short survey asked for feedback on strategies and cue use.

Each trial started with a red fixation cross during a jittered inter-trial interval with an average time of 3 seconds (+/- 0.25 seconds). The cue-stimulus interval was 2.5 seconds long and consisted of a 1.5 second cue (scene label or neutral) followed by a 1 second white fixation cross. The stimulus and response period lasted between 2 and 4 seconds, which included a 2 second item-scene pairing followed by a 2 second white fixation cross. If the participant responded within the 2 second item-scene pairing the next trial began after the item-scene pairing. If the participant did not respond within the 2 second item-scene pairing, they were given up to 2 more seconds to respond during the white fixation cross before the trial ended.

Participants were instructed as follows: “For this task you will be making judgements about the likelihood that an item would appear in the indicated scene (high (1), medium (2), or low (3)), and will respond with the index, middle, and ring fingers of your right hand. Before each item-scene pairing, a cue will indicate one of the four scenes or the neutral cue (“-----”), these are the same you saw in the previous task. For most of the trials with a scene cue, it will ether match the scene presented with the item, or no scene will be presented, and you will have to make your judgement based on the scene indicated by the cue. On a few trials the cue and the presented scene will not match, for those trials, please make your judgements based on the presented scene and not the one indicated at the cue. We will now complete a short practice. The task is mostly not self-paced, please only respond once per trial. Do you have any questions?” If the participant did not understand the task, instructions, or practice, they were repeated until they did. There was no mention of the upcoming memory task.

2.3.3 Retrieval Task

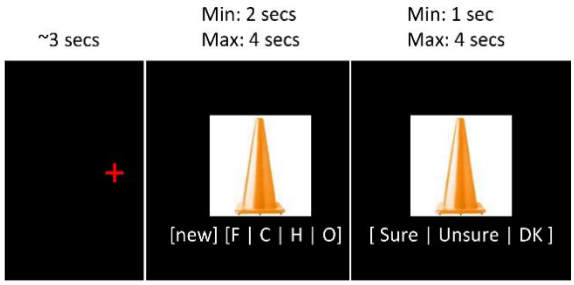

Figure 4: Retrieval Task

The retrieval task consisted of all 400 old items intermixed with 50 new items, shown in Figure 4. Retrieval was spaced across 8 blocks with 50 old trials and 6 to 8 new trials in each block each. Each trial was partially self-paced, and each block took between

4.9 and 8.7 mins with a total possible task time of 39.2 to 69.6 mins (Mean = 51.25 mins, SD = 4.45 mins).

Participants were instructed to indicate if it was a new item or, if it was an old item, which scene the item was paired with during encoding and then rate their confidence in that decision. Each trial started with a red-fixation cross during the jittered inter-trial interval with an average time of 3 seconds (+/- 0.25 seconds) and followed by two retrieval questions. The first question was on the screen for a minimum of 2 and a maximum of 4 seconds. Participants responded with the left index finger on the spacebar to indicate if the item was new. If the item was old, they responded with the 1, 2, 3, and Enter keys on a number pad with the four fingers on their right hand to indicate if the item was paired with the forest, city, house, or office, respectively. The second question was on the screen for a minimum of 1 and a maximum of 4 seconds. Participants responded with the 1, 2, and 3 keys on a number pad with the first three fingers of their right hand to indicate trial confidence (sure, unsure, or don't know, respectively). "Don't Know" was only instructed to be used if the participant knew it was an old item but randomly guessed on which scene it was paired with, if the participant had any information (such as outside or inside), they were instructed to use the low confidence response. The trial automatically continued if no response was made in the allocated time limit. If the participant failed to respond to both questions, the trial was excluded from analysis.

Participants were instructed as follows: "For this part of the study, you will be presented with all the items you saw in the previous task and new items. Your task is to select the scene in which you made the item-scene judgement, or indicate it is a new item. After each response you will indicate if you are sure or not about your response. Each scene

response is mapped to one of the four fingers on your right hand [‘1’,’2’,’3’,’enter’]. If you know that the item is old, but can’t remember which scene it was associated with, please randomly select one of the scene responses. New responses will be indicated with your left index finger [‘space’]. After the first question, please indicate your confidence using the first 3 fingers of your right hand [‘1’,’2’,’3’] which correspond to your index, middle, and ring fingers and the confidence levels: ‘Sure’, ‘Unsure’, or ‘DK’ (i.e. Don’t Know), respectively. If you remember some details about the scene (e.g. indoor or outdoor) but not the exact scene, please use the ‘Unsure’ response. If you truly have no idea which scene the item was associated with, but chose one because you recognized the item, select the ‘DK’ response. The task has some set time limits, as seen in the figure below, please only respond once per trial. We will now complete a short practice. Do you have any questions?” If the participant did not understand the task, instructions, or practice, they were repeated until they did.

2.4 Behavior Analysis

The data are reported for all the conditions, but we limited our statistics and results to valid and invalid conditions and their relationship to the neutral conditions. The required condition was included to reduce the possibility of the participant strategically ignoring the cues during encoding, and not included in the main analysis. Item Memory was assessed with Correct Recognition (Pr) (Snodgrass & Corwin, 1988). Pr (Hits – False Alarms) adjusts memory performance by an individual subject’s false alarm rate (misclassifying a new item as an old item), which makes the ‘at chance’ rate equal to zero. Context memory was assessed as the proportion of all old items where the context scene was correctly identified. Confidence was calculated separately for each condition (valid, invalid, neutral,

required) and level of accuracy (context correct, context incorrect, item miss) as the proportion of trials given a high confidence rating. Reaction times were assessed at both encoding and retrieval. ANOVAs were used to assess differences between all our 3 conditions of interest, and follow-up analyses used paired sample t-tests. Additional analyses across all four conditions are reported in Appendix A. All behavior analyses are Huynh-Feldt corrected, were appropriate.

2.5 EEG Recording

Continuous EEG data was collected from the scalp with 32 Ag-AgCl electrodes using the BioSemi ActiveTwo amplifier system (BioSemi, Amsterdam, Netherlands) and six external electrodes. The external electrodes recorded from the left and right mastoids, left and right lateral canthi, and two electrodes placed superior and inferior to the right eye. Scalp electrodes were placed according to the extended 10-20 system (Nuwer et al., 1998). EEG was sampled at 512 Hz with 24-bit resolution without high or low pass filtering. The ActiveTwo system uses a Common Mode Sense(CMS) active electrode with a Driven Right Leg (DRL) passive electrode instead of a traditional reference and ground, respectively.

2.6 EEG Pre-processing

All EEG data was processed in MATLAB with custom code and the following toolboxes: EEGLAB (Delorme & Makeig, 2004; Delorme et al., 2011), ERPLAB (Lopez-Calderon & Luck, 2014), FIELDTRIP (Oostenveld, Fries, Maris, & Schoffelen, 2011), Aperture (http://mortonne.github.io/aperture/), and the Princeton MVPA toolbox (http://www.pni.princeton.edu/mvpa). Offline, the continuous EEG data was be down

sampled to 256 Hz, bandpass filtered between 0.05 and 125 Hz, and then referenced to the average of the left and right mastoid electrodes.

To investigate lower frequencies, larger epochs are required to account for signal loss during wavelet conversion. During the familiarization task, I epoched the data from 1 second pre-cue onset to 3 seconds post-cue onset with a range of interest from 0.5 seconds pre-cue onset to 2.5 seconds post-cue onset (1 second post scene presentation). During the encoding task, I epoched the data from 1.25 seconds pre-cue onset to 5.5 seconds post cue onset (i.e. 3 seconds post stimulus onset), with a range of interest from 0.5 seconds pre-cue onset to 4.5 seconds post-cue onset (i.e. 2 seconds post-stimulus onset). During the retrieval task, I epoched the data from 1.25 second prestimulus onset to 4 seconds post stimulus onset with a range of interest from 0.5 seconds prestimulus onset to 3 seconds post stimulus onset.

In the time domain, each epoch was baseline corrected to the average amplitude of the whole epoch. Epochs with extreme voltage shifts, or epochs that contain blinks during stimulus onset were removed from the data. Then, ICA was run to identify activity related to ocular artefacts (i.e. blinks and horizontal eye movements), and these were removed from the data. After the removal of ocular artefacts, the data was re-baselined to the -300 to 0-time range and the epochs were visually inspected and removed if additional artefacts were found. If a dataset contained a noisy electrode (e.g. greater than 30% of the data needed to be rejected), it was removed from the dataset before pre-processing and interpolated before converting into the time-frequency representation. Five participants needed on average 1.8 electrodes interpolated (SD=.84), and the proportion of rejected epochs was reasonable: Familiarization task 9.6% (SD= 6.5%), Encoding task 18.7%

(SD=8.3%), and Retrieval task 15.6% (SD=7.2%). Trial counts after artefact rejection: For Familiarization: Study (forest: Mean = 41, SD = 3; city: Mean = 41, SD = 3; house: Mean = 41, SD = 4; office: Mean = 41, SD = 4), Imagine ((forest: Mean = 9, SD = 1; city: Mean = 9, SD = 2; house: Mean = 9, SD = 1; office: Mean = 9, SD = 1). For encoding: Valid (Context Hit: 84, SD = 28; Context Miss: 56, SD=20; Item Miss: 22, SD=14), Invalid (Context Hit: 46, SD = 19; Context Miss: 38, SD=17; Item Miss: 15, SD=10), Neutral (Context Hit: 16, SD = 6; Context Miss: 12, SD=4; Item Miss: 4, SD=3), Required (Context Hit: 15, SD = 7; Context Miss: 11, SD=4; Item Miss: 5, SD=3).

2.7 Time – Frequency Processing

Morlet wavelets (Percival & Walden, 1993) at 5 cycles were used to assess oscillatory power between 2 and 30 Hz. After transformation, each epoch was reduced to the time range of interest and down sampled to 50.25 Hz (Cohen, 2014). For analyses with condition averages, a 10% trimmed mean (Wilcox & Keselman, 2003) for each condition of interest was made for each subject. Frequencies of interest were comprised of theta (4 to 7 Hz), alpha (8 to 12 Hz), and beta (16 to 26 Hz).

2.8 Time – Frequency Significance Testing

For across subject condition differences in the oscillatory data, significance was carried out with spatiotemporal clustering and Monte Carlo permutation tests from the FIELDTRIP toolbox (Blair & Karniski, 1993; Maris & Oostenveld, 2007). Cluster correction for the multiple comparison problem controls the familywise error rate by thresholding individual datapoints before creating clusters of adjacent datapoints. Then the sum of the t-values from each cluster are used to create the cluster level statistic. The Monte

Carlo permutation test creates an expected null distribution of a two-tailed t-statistic by randomly selecting data from each condition of interest and calculating the t-test statistic, then repeating this process 2000 times. Once the expected null distribution is created, the t-statistic from our true conditions of interest is compared to the expected null distribution and considered significant if it falls below an alpha level of .05 for a two-tailed test. Spatiotemporal clusters needed to be reliable over two or more neighboring electrodes and last longer than 0.2 seconds (for similar approaches: Addante et al., 2011; Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013; Hanslmayr et al., 2009; Pastotter, Schicker, Niedernhuber, & Bauml, 2011; Staudigl, Hanslmayr, & Bauml, 2010). For average condition differences, these clusters where identified using paired sample t-tests. For relationships between oscillatory power and performance the same spatiotemporal clustering procedure was used to identify clusters that correlated the specified performance metric. For simplicity and reporting, the average power for each spatiotemporal cluster was used to quantify condition differences and for the reported Pearson correlations between performance and frequency power.

2.9 Multivariate Pattern Analysis

Multivariate pattern analysis was used to investigate whether the scene cues at encoding reactivated the memory representation of the specified scene. For classification analyses I used the Aperture (http://mortonne.github.io/aperture/) and Princeton MVPA (http://www.pni.princeton.edu/mvpa) toolboxes. Classification utilized penalized logistic regression (penalty = 10), with L2 regularization (Duda, Hart, & Stork, 2001). No baseline was applied to the EEG data for the classification analyses. Before classification, in order to reduce feature space, I reduced the data to create consecutive 0.1 second time bins

representing the average power within the time block and averaged across our frequency bands of interest (theta (4 to 7 Hz), alpha (8 to 12 Hz), and beta (16 to 26 Hz)) for each trial. Including all frequency bands, time points, and electrodes for one second of data would have resulted in 237,568 features per trial (29 frequencies * 256 time points * 32 electrodes), which was computationally expensive. Each classification was resampled and repeated 500 times to gain reliable estimates of classifier performance and estimates of evidence for each regressor level (i.e. scene). The average classifier performance estimates are reported.

Using the four scenes (forest, city, house, office) as regressor values sets the theoretical chance performance value to 25%, and a one sample t-test against this chance value was used to assess reliability for each classification analysis. In order to verify that a 25% chance value was robust within the current sample, a classifier analysis with scrambled (randomized) regressor labels was assessed for each subject. The mean classification value was calculated for each participant across 500 scrambled iterations. Then across all participants, I tested the mean randomized classification values against the expected chance value (0.25). On average the familiarization task included 41 trials (SD = 4) per scene (or cue), and the encoding task included on average 56 trials (SD= 10) for each cue label.

2.9.1 Familiarization Task Classification

For the familiarization task, classification was performed on both the cue and stimulus (i.e. scene presentation) time periods of each study trial. Before the selection of features, the feature space included all 32 head electrodes, 3 frequency bands (theta, alpha,

beta), and 10 consecutive time points (0.1 second each, 1 second total), which resulted in a total of 960 features per epoch for each classification analysis (i.e. cue or stimulus). One second of time data was used to limit the possible influence of stimulus activity being captured in the cue – stimulus interval due to temporal smearing of the wavelet transformed EEG, and due to limitations in epoch length for the stimulus interval.

Cross validation was done at the block level with four training blocks and one testing block, such that each block served as the testing block once and part of the training data four times. In addition, a pattern to pattern classification analysis was performed where the classifier was trained on the study trials, either cue or stimulus, and tested on the imagine trials during the scene label presentation.

A second round of classification analyses was performed on the familiarization task to identify channel and frequency features that contributed the most to classification accuracy. Each step of the feature selection process used the same cross validation procedure on the study trials (train on four blocks and test on one). Time was not assessed during feature selection. The first step of feature selection included all three frequency bands and iterated over the 32 electrodes. In order to identify which electrode's classification accuracy values clustered together, a hierarchical cluster analysis was performed with between-groups linkage and squared Euclidean distance. No standardization was done on the classifier performance values, and the cluster analysis was set to return two to five solutions. During the second step classification was iterated across the three frequency bands for all 32 electrodes and each identified electrode cluster.

2.9.2 Encoding Task Classification

For the encoding task, classification was performed on valid and invalid trials with correct item memory. Neutral, required, and item memory miss trials were excluded from classification analysis as the hypotheses were directly related to the reactivation of the scenes on successful or unsuccessful context memory for valid and invalid trials. Classification analyses were trained on both the cue and the stimulus period of the familiarization task study trials and each was tested on the encoding cue and stimulus time period, respectively. Multiple classification analyses were run that utilized all the channel and frequency features, as well as those identified through the feature selection process of the familiarization task. Classification accuracy was assessed as a function of condition (valid and invalid) and memory performance (context correct, context incorrect), as well as across participant correlations between classifier accuracy and the proportion of correct valid and invalid context memory judgements. Overall classifier accuracy was correlated with the validity effect (valid – invalid context hit proportion), and the classifier accuracy for invalid context misses was correlated with the proportion of invalid lure misses. One participant was removed from the correlation between classifier accuracy and the validity effect for having a validity effect greater than 3 standard deviations away from the mean.

CHAPTER 3. RESULTS

3.1 Familiarization Task

3.1.1 Behavior

During the familiarization task, response accuracy and reaction times were recorded. For neutral trials participants correctly responded on 88.6% (SD=6.1%) of trials on the study phase and 95.9% (SD=9.6%) of the time during the imagine phase. Reaction times for neutral trials during the study phase were 0.691 seconds (SD=0.174 seconds), and during the imagine phase was 0.643 seconds (SD=0.212 seconds). For scene trials, during the study phase participants correctly classified the scene image 98.6% (SD=1.3%) of the time with an average reaction time of 0.711 seconds (SD=0.237 seconds). During the imagine phase, a 'high quality' response was given 82.6%(SD=13.8%) of the time, with an average reaction time of 0.816 seconds (SD=0.279 seconds). These numbers suggest that the participants were engaged and responded appropriately during the task.

3.1.2 MVPA

The familiarization task EEG data was used for training the MVPA classifier to test during the encoding task. To assess classifier accuracy within the familiarization task multiple classifiers were ran to assess overall classification with the cue and stimulus time periods. An additional set of classifiers were ran to select feature sets for testing on the encoding data. A visual representation of the classifier accuracy across frequency band and electrodes can be found in Figure 5.

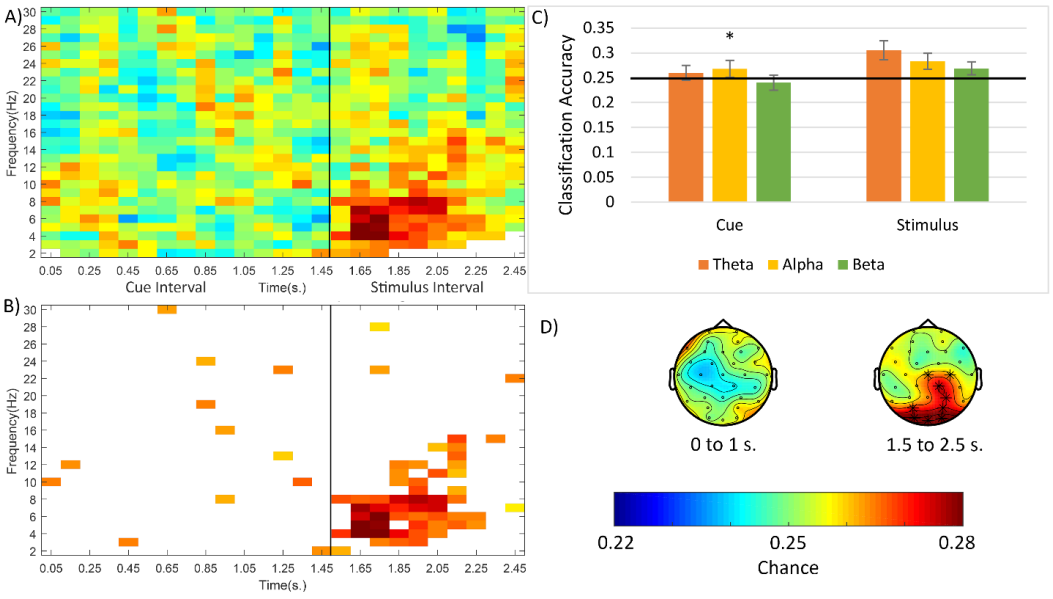

Figure 5: Classification accuracy for cross validation of study cues during familiarization task. Chance = 0.25. Heat maps: Cue onset is at zero, Stimulus onset is at 1.5 seconds (black line). A) Pattern included all 32 channels. All frequencies 2 to 30 Hz and 25 time bins (0.1 second in each time bin). B) Frequency by time bin pairs where the 95% confidence interval did not include chance. C) Patterns included all 32 channels and time points with each cue and stimulus interval, for each frequency band. Error bars = 95% confidence interval. D) Pattern includes all 3 frequency bands, and 10 time points for each cue and stimulus interval, for each channel. Channels where the 95% confidence interval did not include chance are marked with circles.

3.1.2.1 Cue Interval

During the familiarization cue interval, a feature set that included all 32 electrodes, 3 frequency bands, and 1 second of data (10 0.1 second time intervals) was unable to successfully discriminate between the cue labels (Mean=0.253, SD=0.005) [t(24)=0.523, p=0.606]. The results of the scrambled classifier analysis found the cue period (Mean=0.25, SD=0.001, CI<0.001) [t(24)=-0.778, p=0.444] was not inherently different from chance. Unsurprisingly, training on this cue period feature set was not able to successfully classify

the imagine trials of the familiarization task (Mean=0.258, SD=0.082) [t(24)=0.509, p=0.615].

Feature selection across all 32 electrodes and iterated across frequency band found above chance performance within the alpha frequency band (Mean=0.268, SD=0.042) [t(24)=2.092, p=0.047]. Neither the theta (Mean=0.26, SD=0.036) [t(24)=1.365, p=0.185], nor the beta (Mean=0.24, SD=0.037) [t(24)=-1.311, p=0.202] frequency bands where significantly different from chance classifier performance.

Feature selection across the three frequency bands and iterated across all 32 electrodes identified 4 electrode clusters as seen in Table 1. Significant above chance performance was found within frontal alpha [t(24)=2.335, p=0.028] and right frontocentral alpha [t(24)=2.765, p=0.011]. Significant below chance performance was found in right frontocentral beta [t(24)=-2.927, p=0.007], and marginal below chance performance was found in posterior beta [t(24)=-1.924, p=0.066].

Table 1: Classification accuracy for each identified cluster during the cue – stimulus interval

	All Frequencies	Theta	Alpha	Beta
Frontal (Fp1 AF3 F7 T7 T8 F4 F8 AF4 Fp2)	0.260[0.041]	0.255[0.037]	0.268[0.038]*	0.248[0.028]
Central (F3 FC1 FC5 C3 CP1 CP5 P7 P3 Pz PO3 CP2 FC2 Fz Cz)	0.244[0.028]	0.255[0.033]	0.248[0.029]	0.240[0.033]
Posterior (O1 Oz O2 PO4 P4 P8 CP6)	0.256[0.034]	0.254[0.029]	0.259[0.035]	0.236[0.036]+
Right Frontocentral (C4 FC6)	0.249[0.038]	0.253[0.027]	0.265[0.028]*	0.233[0.029]**

Note: Mean [SD]. + = p < 0.1, * = p < 0.05, ** = p < 0.01, *** = p < 0.001; Feature sets include 1 second of data from cue onset (10 0.1 second intervals)

Only the right frontocentral alpha cluster (Mean=0.278, SD=0.062) [t(24)=2.242, p=0.034] was able to reliably classify the imagine trials above chance. Additionally, the

frontal beta cluster was significantly below chance (Mean=0.225, SD=0.058) [t(24)=-2.14, p=0.043].

3.1.2.2 Stimulus (Scene) Interval

During the familiarization stimulus (i.e. scene) interval, a feature set that included all 32 electrodes, 3 frequency bands, and 1 second of data (10 consecutive 0.1 second time intervals) was able to successfully discriminate between the four scene stimuli (Mean=0.309, SD=0.048) [t(24)=6.189, p<0.001]. The results of the scrambled classifier analysis found the stimulus period (Mean=0.251, SD=0.002, CI=0.001) [t(24)=1.713, p=0.1] was not inherently different from chance. Although training on the stimulus period feature set was not able to successfully classify the imagine trials of the familiarization task (Mean=0.265, SD= 0.075) [t(24)=0.984, p=0.335].

Feature selection across all 32 electrodes and iterated across frequency band found above chance performance within the theta (Mean=0.297, SD=0.048) [t(24)=4.884, p<0.001], alpha (Mean=0.278, SD=0.047) [t(24)=2.924, p=0.007], and beta (Mean=0.271, SD=0.029) [t(24)=3.595, p=0.001] frequency bands. Feature selection across the three frequency bands and iterated across all 32 electrodes identified three clusters, which were nearly all above chance, as seen in Table 2.

Table 2: Classification accuracy for each identified cluster during the post -stimulus interval

	All Frequencies	Theta	Alpha	Beta
Frontocentral (Fp1 AF3 F7 F3 FC1 FC5 T7 C3 CP1 CP5 P7 P3 CP6 CP2 C4 T8 FC6 FC2 F4 F8 AF4 Fp2 Fz Cz)	0.278[0.043]**	0.266[0.043]+	0.269[0.028]**	0.263[0.032]*
Parietal (Pz PO4 P4 P8)	0.283[0.051]**	0.277[0.041]**	0.268[0.039]*	0.257[0.028]
Occipital (PO3 O1 Oz O2)	0.307[0.061]***	0.289[0.052]***	0.270[0.041]*	0.275[0.027]***

Note: Mean [SD]. + = p < 0.1, * = p < 0.05, ** = p < 0.01, *** = p < 0.001; Feature sets include 1 second of data from stimulus onset (10 0.1 second intervals)

None of these electrode clusters were able to classify the imagine trials within or across frequency bands: frontocentral [absolute t's < 1.5, p's > 0.14], parietal [absolute t's < 0.97, p's > 0.34], and occipital [absolute t's < 0.54, p's > 0.59].

3.1.2.3 Summary

For the familiarization cue period, classifier performance was above chance within the alpha frequency band, which was strongest across the frontal electrodes. For the familiarization stimulus period, classifier performance was above chance across all 32 electrodes both across and within each frequency band. Cluster analysis revealed three groups of electrodes in which nearly all classification analyses were significantly above chance (beta frequency band within the parietal cluster was almost marginal).

3.2 Encoding Task

3.2.1 Behavior

Performance data for valid, invalid, neutral, and required trials are reported in Tables 3, 4, 5, and 6. As required trials were only included to maximize the likelihood of participants using the cues, the following behavioral analyses include valid, invalid, and neutral cue conditions (though subsequent analyses including required trials can be found

in Appendix A). Behaviorally I predicted that valid trials would have higher context memory performance and faster reaction times. Since the cue information was directed at the level of context memory and not item memory, I predicted that item memory would not differ between the valid and invalid conditions.

Table 3: Memory Performance

Condition	Valid		Invalid		Neutral		Required	
Correct Recognition (Pr)	0.676	[0.185]	0.655	[0.210]	0.667	[0.192]	0.643	[0.202]
Item Hits	0.867	[0.086]	0.846	[0.113]	0.858	[0.086]	0.834	[0.116]
Context Correct	0.519	[0.153]	0.464	[0.190]	0.487	[0.157]	0.466	[0.181]
Context Incorrect	0.348	[0.122]	0.382	[0.171]	0.371	[0.121]	0.369	[0.123]
Proportion Context Correct	0.594	[0.146]	0.542	[0.197]	0.562	[0.148]	0.545	[0.166]

NOTE: Mean [SD]. Proportion Context Correct = Context Correct / Item Hits. Context Memory Chance performance = 0.25 (4 scenes)

3.2.1.1 Item Memory

Consistent with my predictions regarding item memory, a 3 Condition (valid, invalid, neutral) ANOVA did not reveal significant differences in Pr between the conditions [$F(2,48)=1.297$, $p=0.280$, $\eta p2=0.051$, $\beta=0.241$], see Table 3.

3.2.1.2 Context Memory

For context memory, I predicted that performance would be greater for valid compared to invalid trials, see Table 3. The results of a 3 Condition (valid, invalid, neutral) ANOVA on the proportion of context memory hits out of item memory hits (context correct / item hits) found a marginal difference between these conditions [$F(2,48)=2.610$, $p=0.100$, $\eta p2=0.098$, $\beta=0.426$]. Follow-up analyses found significantly greater context memory performance for the valid compared to the neutral condition [$t(24) = 2.251$, $p = 0.034$], and marginally greater context memory performance for the valid compared to the invalid

condition [t(24) = 1.993, p = 0.058]. The neutral and invalid conditions did not differ in context memory accuracy [t(24) = -0.753, p = 0.459].

3.2.1.3 Proportion of Selected Invalid Lures

Given the marginal effect of validity on context memory performance, I investigated if participants were more likely to select the invalid lure (cued scene) than the other incorrect scenes during the invalid context miss trials. The invalid lure scene was selected on average 42.9% (SD= 9.3%) of the time and the results of a one-sample t-test confirmed that this was above chance (3 incorrect scene options = 33%) [t(24)=5.271,p<0.001] , see Table 4.

Table 4: Proportion of incorrect context memory responses for each scene

Cued Scene	Valid		Invalid All		Invalid Select Cue		Invalid Select Other	
Forest	0.211	[0.083]	0.279	[0.057]	0.098	[0.070]	0.101	[0.070]
City	0.245	[0.090]	0.231	[0.055]	0.103	[0.050]	0.167	[0.080]
House	0.370	[0.116]	0.252	[0.066]	0.140	[0.067]	0.204	[0.088]
Office	0.174	[0.092]	0.238	[0.069]	0.088	[0.059]	0.100	[0.059]
Overall	1		1		0.429		0.572	

NOTE: Mean [SD]. Valid and Invalid All: proportion of incorrect context memory judgements by cued scene. Invalid Select Cue: Proportion of invalid misses when the invalid lure (cued) scene was selected. Invalid Select Other: Proportion of invalid misses when the cued scene wasn't selected

3.2.1.4 Proportion of High Confidence Responses

I also investigated the proportion of high confident responses, see Table 5. If the invalid lure cue interfered with successfully encoding the item – scene pairing, then I expected less high confident responses for invalid trials. The results of a 3 Condition (valid, invalid, neutral) ANOVA on the proportion of high confidence judgements within correct context memory judgements found a marginally significant effect of condition

[F(2,48)=3.036, p=0.057, ηp2=0.112, β=0.561]. Follow-up analyses revealed that the proportion of high confidence hits was greater for the valid compared to the invalid condition [t(24) = 2.073, p = 0.049], but the valid context correct condition compared to the neutral condition was not significant [t(24) = 0.245, p = 0.809], and invalid compared to neutral was marginally significant [t(24) = -1.944, p = 0.064]. Thus, I found evidence that participants were less confident in the invalid condition when they selected the correct context scene at retrieval compared to both valid and neutral conditions. Invalid context misses contain a mixture of lures (cued scenes) and non-lures (other incorrect responses). I further invested high confidence responses for invalid context misses for the lures (Mean = 0.374, SD=0.305) and non-lures (Mean=0.277, SD=0.272), the results of a t-test found a greater proportion of high confidence responses for lures compared to non-lures [t(24)=2. 955, p = 0.007].

Table 5: Proportion of High Confidence Responses

Condition	Context Correct		Context Incorrect		Item Miss	
Valid	0.743	[0.152]	0.3	[0.269]	0.461	[0.283]
Invalid	0.684	[0.199]	0.323	[0.278]	0.503	[0.276]
Neutral	0.737	[0.195]	0.318	[0.252]	0.526	[0.301]
Required	0.665	[0.179]	0.277	[0.267]	0.504	[0.346]

NOTE: Mean [SD].

3.2.1.5 Reaction Times

In line with previous cueing studies with invalid cues I predicted that during encoding the valid condition would be faster than the invalid condition (for review: Petersen & Posner, 2012). The results of a 3 Condition (valid, invalid, neutral) x 2 Accuracy (context correct, context incorrect) ANOVA revealed a significant main effect

of condition [F(2,48)=16.775, p < 0.001, ηp2=0.411, β=0.995], and accuracy [F(1,24)=5.357, p=0.030, ηp2=0.182, β=0.603], but not the interaction [F(2,48)=0.218, p=0.747, ηp2=0.009, β=0.079]. Follow-up t-tests found the valid condition was significantly faster than the neutral [t(24)=-4.033, p<0.001] and invalid [t(24)=-7.886, p<0.001] conditions. Reaction times for invalid and neutral conditions were not significantly different [t(24) = 1.556, p = 0.133]. To test if the validity effects found for context memory and reaction time were related, I correlated the validity differences (valid – invalid) on the proportion of correct context memory judgements and reaction times [r(23) = 0.162, p = 0.440]. Follow-up analysis between invalid context incorrect lures compared to non-lures did not reveal significant differences for encoding reaction times [t(24)=-0.614, p=0.545]. These results suggest that cue validity may have facilitated perception of the scene, regardless of subsequent context memory accuracy, see Table 6.

Table 6: Encoding Reaction Times

	Context Correct		Context Incorrect		Item Miss	
Valid	1.396	[0.262]	1.365	[0.260]	1.345	[0.288]
Invalid	1.528	[0.290]	1.495	[0.286]	1.522	[0.324]
Neutral	1.493	[0.266]	1.442	[0.228]	1.443	[0.343]
Required	1.483	[0.361]	1.559	[0.362]	1.479	[0.449]

NOTE: Mean [SD], In seconds.

3.2.2 Neural activity during the encoding cue – stimulus interval

During the cue -stimulus interval at encoding I predicted that retrieval of the cued scene would facilitate context memory performance for valid trials and interfere with context memory performance for invalid trials. In line with this hypothesis I found behavioral evidence that the invalid cue was interfering with context memory performance.

Thus, I expected that the neural correlates of retrieving the cued scene to be positively related to valid and negatively related to invalid context memory performance. For the univariate analyses, I predicted that greater theta synchronization and greater alpha desynchronization would be related to higher context memory performance for valid trials, while invalid trials would have the opposite pattern. For the MVPA, I predicted that reactivation of the scene in response to the encoding label cues would be positively related to performance on valid trials and negatively related to performance on invalid trials. To test for reactivation of the scene cues at encoding, I used the familiarization task study cue as the training dataset and the encoding cue period as the test dataset.

Results from the spatiotemporal cluster analyses did not identify any significant prestimulus differences in average frequency power between context hits and misses for valid or invalid trials. Very few MVPA classification values were above chance and a full table with all classification values by condition, memory performance, and feature set can be found in Appendix D, Table 9.

3.2.2.1 Pre-stimulus alpha correlates with valid context memory

For valid trials, a significant negative correlation was found between alpha power in the valid context memory contrast and the proportion of valid context memory hits across a cluster of 16 left posterior electrodes (1.8 to 2.7 seconds post-cue) [$r(23)=-0.581$, $p=0.002$]. The analogous spatiotemporal cluster for the invalid condition was not significant [$r(23)=-0.085$, $p=0.686$], and the correlation coefficients were marginally differed from each other [Fisher's $p=0.055$], see Figure 6. Removal of one outlier

participant did not change the pattern of results for either the valid [r(22)=-0.462, p=0.023], or invalid [r(22)=0.153, p=0.475] conditions.

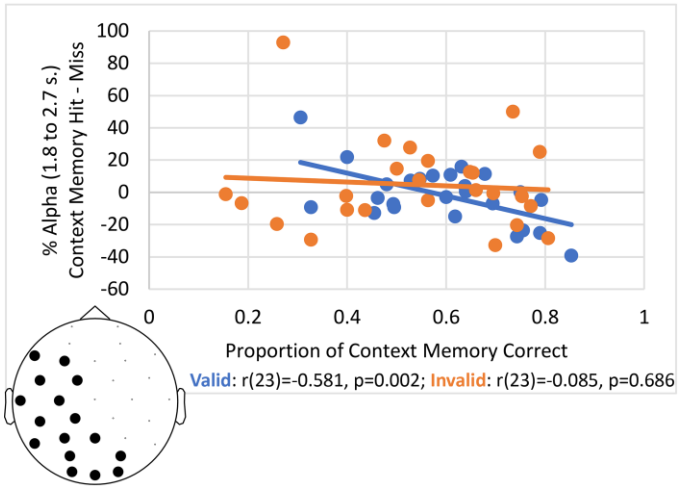

Figure 6: Prestimulus Alpha. Valid: [r(23)=-0.581, p=0.002]. Invalid: [r(23)=-0.085, p=0.686]

Given that reaction times were faster for valid trials than invalid trials, the greater alpha desynchronization for correct context memory may reflect the successful retrieval of the cued scene. Neither valid [r(23)=-0.14, p=0.506] nor invalid [r(23)=0.218, p=0.296] context correct trial reaction times correlated with alpha power. The difference between correct and incorrect reaction times for valid trials marginally correlated with the alpha effect for valid trials [r(23)=-0.377, p=0.063], while the same relationship was not found for invalid trials [r(23)=-0.059, p=0.78]. Additionally, if this prestimulus alpha effect was only associated with attentional processes and not memory retrieval or reactivation, I would have expected to find a correlation in either direction for the invalid condition. Unfortunately, the task was not designed to tease apart attention and memory retrieval within the alpha frequency band, and any conclusions about the exact contributions of either process remains speculative.

3.2.2.2 Discrimination of the cued scene support valid and interferes with invalid context memory

For the classification analysis that included all 32 electrodes, 3 frequency bands, and 1 second (10 0.1 second intervals) classification accuracy was not significantly above chance. Correlations between the proportion of correct context memory and classification was marginally significant for the invalid condition [r(23)=-0.353 p=0.084], and not significant within the valid condition [r(23)=0.282 p=0.172], as seen in Figure 7. In addition, the proportion of selected invalid lures did not correlate with classification accuracy within invalid context misses [r(23)=0.108 p=0.608], and overall classification accuracy did not correlate with the validity effect [r(22)=-0.54, p =0.802].

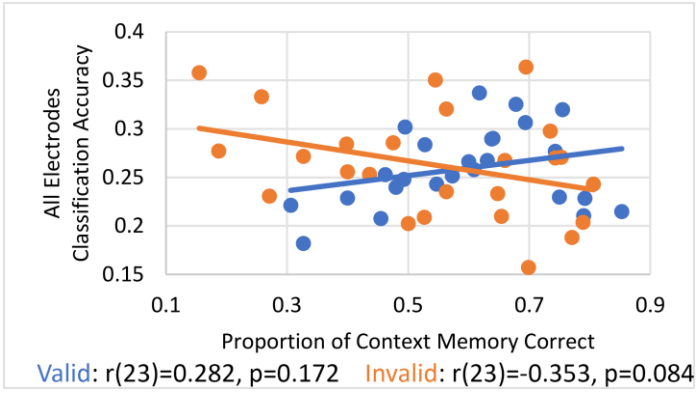

Figure 7: Correlations between the classification of valid trials and proportion of valid context hits compared to the classification of invalid trials and the proportion of invalid context hits. Feature space includes all 32 electrodes, 3 frequency bands, and 1 second from cue onset

The feature selection analyses are restricted to those features identified during cross validation of the familiarization cue, see above. Within the alpha frequency band, classifier accuracy was greater than chance for invalid context hits across all electrodes (Mean=0.281, SD=0.072) [t(24)=2.162, p=0.041], and marginally within the frontal cluster

(Mean=0.278, SD=0.079) [t(24)=1.754,p=0.092]. Marginal positive correlations between the proportion of valid context memory hits and classification accuracy were found for the frontal [r(23)=0.363 p=0.075], and right frontocentral [r(23)=0.375 p=0.065] clusters, but the invalid condition did not show a relationship to classification accuracy [absolute r's < 0.13, p's > 0.5], as seen in Figure 8. Although, the proportion of selected invalid context lures positive correlated with classification accuracy for invalid context misses within the frontal alpha cluster, as seen in Figure 8. No correlations between the identified feature sets and the validity effect were found [absolute r's < 0.22, p's > 0.3].

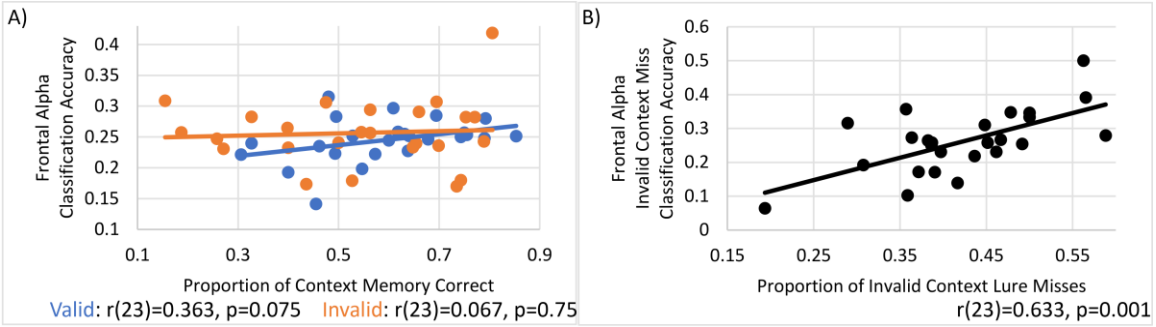

Figure 8: Correlations for classification accuracy within the frontal alpha cluster with A) the proportion of context hits for the valid and invalid conditions and B) the proportion of invalid context misses where the cued lure was selected at retrieval.

3.2.2.3 No evidence of reactivation for the familiarization scene during the encoding cue

The previous analyses suggest that the discriminability of the encoding cue is related to memory performance, and the cue information was used to selectively prepare for the upcoming item – scene pairing. In-order to directly test for reactivation of the cued scene, I trained classifiers on the familiarization task scene presentation and tested on the encoding cue. A full table with classifier values can be found in Appendix D, Table 11. A

feature set of all 32 channels, 3 frequency bands, and 10 time points (1 second from onset) failed to successfully classify the encoding cue above chance (Mean=0.243, SD=0.023) [t(24)=-1.595,p=0.124], and none of the condition by memory performance conditions were significantly above chance [absolute t's < 1.2, p's > 0.25]. In addition, correlations between classifier accuracy and memory performance were not reliable [absolute r's < 0.23, p's > 0.28]. Investigating the identified features also failed to find significant above chance performance for classifier accuracy. Correlations between the feature sets and memory performance were also unreliable: frontocentral [absolute r's < 0.26, p's > 0.22], parietal [absolute r's < 0.34, p's > 0.11], or occipital [absolute r's < 0.25, p's > 0.23].

3.2.2.4 Summary

For valid trials, alpha desynchronization leading up to stimulus onset was found to correlate with successful context memory performance. Given that the time course is consistent with expectation of a stimulus (for review: Luck et al., 2000; Petersen & Posner, 2012; Posner & Petersen, 1990), this desynchronization could reflect both attentional orienting (Hamm, Dyckman, McDowell, & Clementz, 2012; Klimesch, 2012; Macdonald, Mathan, & Yeung, 2011; Mazaheri et al., 2014; Zanto et al., 2011), and the retrieval of the specific scene details (Khader & Rösler, 2011). Interestingly, the classification accuracy within the alpha frequency band was positively related to valid context memory performance, suggesting that alpha band activity is likely a result of using the cues to retrieve the associated scene from memory. For the invalid trials I had predicted that there would be evidence of retrieval induced interference. The univariate analysis failed to find evidence of this. But, the MVPA revealed that classification accuracy for invalid cue misses positively corrected with the proportion of invalid lure scenes selected, and overall

classification accuracy was negatively related to invalid context memory performance. These results suggest that for invalid trials, reactivation of the cued scene led to worse invalid context memory performance and an increase in the likelihood of selecting the invalid lure scene at retrieval.

3.2.3 Neural activity during the encoding post-stimulus interval

Under the hypothesis that invalid lure cue would interfere with context memory encoding. I expected to find evidence of greater post-stimulus encoding demands for successfully encoding invalid compared to valid trails. Specifically, I predicted greater theta synchronization and greater alpha/beta desynchronization for invalid compared to valid trials. Assuming the cued scene representation is carried into the post-stimulus interval, then the neural pattern during stimulus onset will likely contain a mixture of both the retrieved scene and the presented scene. Thus, for the MVPA analysis, I predicted greater classification accuracy for valid trials than invalid trials. To test for reactivation of the presented scene at encoding, I used the familiarization task study scene presentation period as the training dataset and the encoding stimulus period as the testing dataset. As with the cue period, a full table with all classification values by condition, memory performance, and feature set can be found in Appendix D, Table 10.

Results from the spatiotemporal cluster analyses did not identify any significant post-stimulus correlations between context memory performance and frequency power for either the valid or invalid conditions. Spatiotemporal clustering also failed to find context memory differences for valid trials.

3.2.3.1 Greater beta desynchronization for successful invalid context memory encoding

For invalid trials, significantly greater beta desynchronization was found for context memory hits compared to context memory misses in a cluster of 20 central and posterior electrodes from 3.75 to 4 seconds post-cue (1.25 to 1.5 seconds post-stimulus) [$t(24)=-3.526, p=0.003$]. Follow up analyses found the same cluster was not significant for valid trials [$t(24)=-0.859, p=0.374$], and the invalid context memory contrast was significantly larger than valid context memory contrast [$t(24)=2.380, p=0.032$], see Figure 9. Given that the invalid incorrect context memory responses contain lures (the cued scene), I reran the identified invalid beta cluster with non-lure context misses. One participant was removed for having to few non-lure misses. The invalid context memory cluster remained significant [$t(23)=-3.176, p=0.002$], although the difference between the invalid and valid context memory contrasts was slightly attenuated [$t(23)=1.764, p=0.086$]. Given that reaction times at encoding were in a similar time period (~ 1.4 seconds from stimulus onset or 3.9 seconds from cue onset), it is possible that beta activity is reflecting the motor response. I correlated the beta power cluster with encoding reaction times but failed find a significant relationship between them for either valid, invalid, or the difference between them [absolute $r's < 0.25$, $p's > 0.22$]

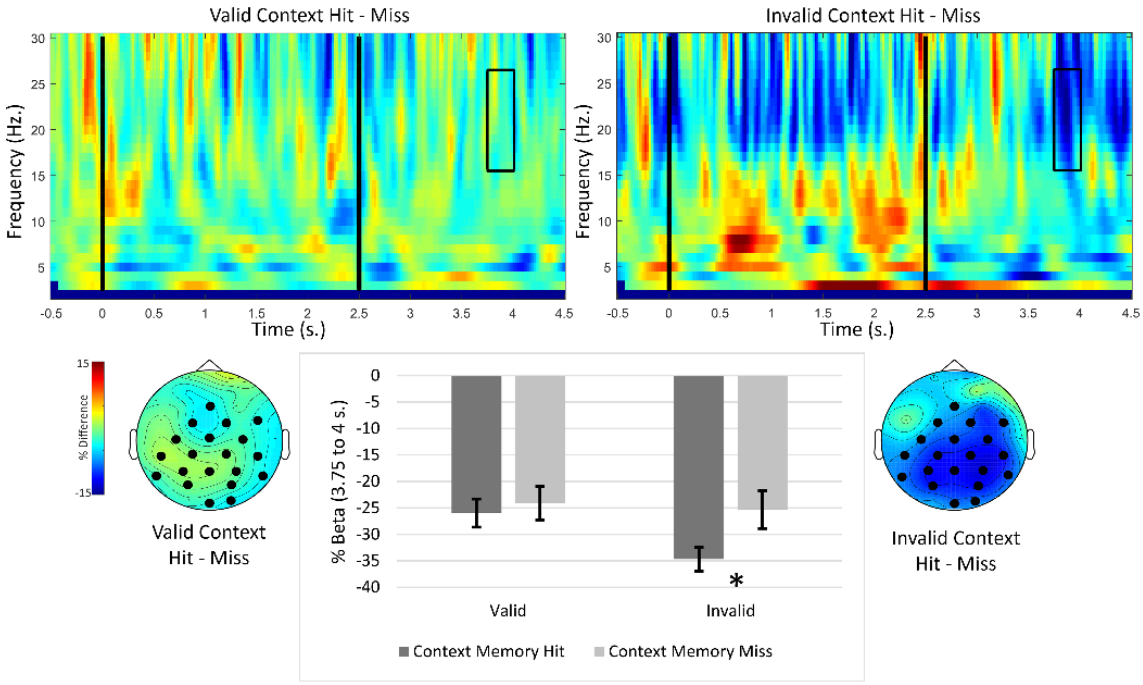

Figure 9: Error bars = 1 SEM. '*' = p < 0.05. Heat maps are comprised of the average cluster power for the significant electrode cluster (highlighted in the topographic maps). Cue onset = 0 seconds, Stimulus onset = 2.5 seconds

3.2.3.2 Invalid cue interfered with processing the presented scene

Classification across all features (32 electrodes, 3 frequency bands, 1 second from stimulus onset) found classification accuracy was significantly above chance for all valid trials (Mean=0.262, SD=0.028) [t(24)=2.062, p=0.05], but not invalid trials (Mean=0.244, SD=0.044) [t(24)=-0.649, p=0.523]. These classification values where marginally different from each other [t(24)= 1.717, p=0.099]. No correlations between classification accuracy or performance were found with all features.

Similar to the encoding cue period, I assessed classification accuracy based on the feature selection processes during the familiarization stimulus presentation. Across all trials (ignoring context memory performance) I found marginally higher than chance

performance across all electrodes within the alpha frequency band for valid trials (Mean =0.26, SD=0.028) [t(24)=1.731, p=0.096], but not invalid trials (Mean =0.252, SD=0.046) [t(24)=0.237, p=0.815]. Within the occipital cluster the valid condition was significantly above chance across all frequency bands (Mean =0.272, SD=0.043) [t(24)=2.536, p=0.018], and marginally higher within the theta frequency (Mean =0.263, SD=0.036) [t(24)=1.779, p=0.088]. Within the occipital cluster the invalid condition was not significantly above chance across all frequency bands (Mean =0.256, SD=0.033) [t(24)=0.974, p=0.34], but was significantly higher within the theta frequency (Mean =0.261, SD=0.025) [t(24)=2.12, p=0.045]. Neither of these effects were significantly different between valid and invalid trials [absolute t's < 1.5, p's > 0.15].

Correlations between memory performance and the identified feature sets can be seen in Figure 10. I found the proportion of valid context memory hits correlated with the occipital electrode cluster across the 3 frequency bands [r(23)=0.398, p=0.049], while the same relationship was not found for the invalid condition [r(23)=0.123, p=0.558]. Within the feature set of the parietal electrode cluster within the theta frequency band the classification accuracy correlated positively with the proportion of correct invalid context memory judgements [r(23)=0.486, p=0.014] (valid: [r(23)=0.218, p=0.296]), and negatively correlated with the proportion of invalid context lure misses [r(23)=-0.386, p=0.056]. I also found a positive correlation between the context validity effect and classification accuracy with the beta frequency band in two electrode clusters: parietal [r(22)=0.439, p=0.032] and occipital [r(22)= 0.412, p=0.045]. Within the alpha frequency band of the frontocentral cluster there was a marginal negative correlation with the validity effect [r(22)=-0.373, p=0.073].

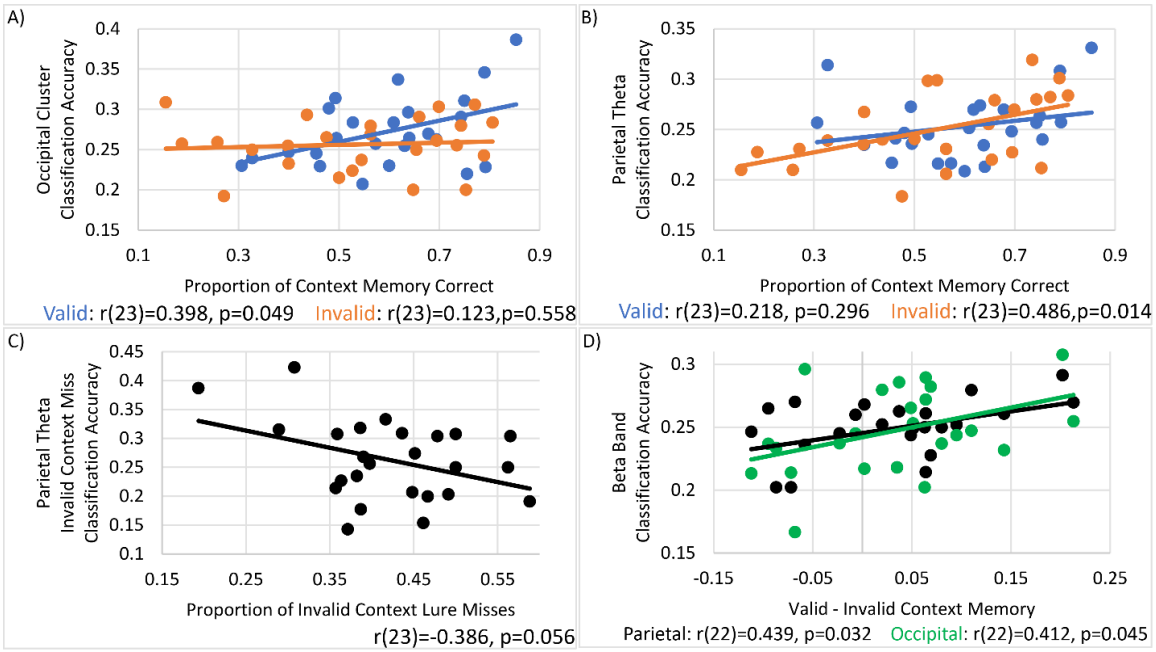

Figure 10: A) Classification accuracy across all frequency bands within the occipital cluster correlated with the proportion of context memory hits within the valid and invalid conditions. B) Classification accuracy within the theta frequency band within the parietal cluster correlated with the proportion of context memory hits within the valid and invalid conditions. C) Classification accuracy within the theta frequency band and the parietal cluster for invalid context memory misses correlated with the proportion of invalid context memory lure misses. D) Classification accuracy within the beta frequency band for both the parietal and occipital electrode clusters correlated with the validity effect (valid – invalid proportion of correct context memory judgements)

3.2.3.3 Summary

I did not find an effect of post-stimulus theta or alpha power for successful context memory encoding compared to unsuccessful context memory for either valid or invalid trials. For invalid trials, I found greater posterior beta desynchronization for context hits than context misses in a late time period. Follow-up analyses found these effects were not driven solely by the inclusion of invalid lures in the invalid context miss condition. Beta desynchronization in the absence of alpha desynchronization may suggest that the attentional demands of post-stimulus encoding did not differ between successful and

unsuccessful context memory. Previous research suggests fluctuations in beta power may reflect top-down control processes involved in predictive coding or signaling the status quo (Engel & Fries, 2010), and beta desynchronization is found in response to violations of expectation (Arnal et al., 2011). The differences between beta desynchronization for the invalid context memory contrast may be related to successfully signaling the violation of the expected scene and updating mental representation. For valid trials, no violation of expectation occurred and there was no need to signal a process of updating the mental representation.

The MVPA, found support for the prediction that the invalid cue would interfere with successfully encoding the item-scene pairing during encoding. Across all electrodes and frequency bands classification accuracy was slightly greater for valid compared to invalid trials across a feature set that included all electrodes and frequency bands and may be maximal over the occipital electrode cluster. Classification accuracy within the occipital electrode cluster positively correlated with successful context memory performance for valid trials. For invalid trials, greater classification accuracy for theta power within the parietal electrodes was associated with higher context memory performance and a lower probability of selecting the invalid cue at retrieval. Finally, classification accuracy in both posterior clusters (parietal and occipital) positively correlated with the validity effect. In sum, this suggests that the invalid lure scene interfered with the neural representation found when processing the presented scene, supporting the interference hypothesis.

3.3 Retrieval

At retrieval I did not predict reaction time differences between the conditions, but longer reaction times during invalid trials could be a result of the increased size of the memory representation (both the target and the invalid lure scenes), or additional evaluation processes involved in selecting the correct scene. As my hypotheses were about context and not item memory I had no predictions involving new items at retrieval, but the data are reported below for the interested reader.

For the EEG, I predicted greater theta synchronization and greater alpha/beta desynchronization for context hits compared to context misses for the valid condition. In addition, I proposed three possible outcomes based on how interference from the invalid lure was resolved. If it was completely resolved at encoding, then I would not expect differences between valid and invalid trials at encoding. If both the target and lure scenes are retrieved and evaluated, then I expected greater context memory effects for the valid compared to the invalid condition. Lastly, retrieving both the target and lure scenes would increase the likelihood of selecting the incorrect scene and greater activation may reflect a subsequent forgetting effect.

3.3.1 Behavior

3.3.1.1 Old Item's Reaction Times

At retrieval, reaction times were assessed with a 3 Condition (valid, invalid, neutral) x 2 Accuracy (context correct, context incorrect) ANOVA revealed a significant main effect of accuracy [$F(1,24)=27.849$, $p<0.001$, $\eta p2=0.537$, $\beta=0.999$], but not condition

[F(2,48)=0.531, p=0.538, ηp2=0.022, β=0.108] or a condition by accuracy interaction [F(2,48)=0.809, p=0.428, ηp2=0.033, β=0.165], see Table 7. Follow-up analyses revealed that context correct was significantly faster than context incorrect trails [t(24)=-5.558, p < 0.001], across all conditions. Follow-up analysis between invalid context incorrect lures compared to non-lures did not reveal significant differences for retrieval reaction times [t(24)=0.379, p=0.708]

Table 7: Retrieval Reaction Times

	Context Correct		Context Incorrect		Item Miss	
Valid	1.938	[0.329]	2.295	[0.375]	1.871	[0.365]
Invalid	1.994	[0.373]	2.279	[0.393]	1.900	[0.398]
Neutral	1.940	[0.337]	2.271	[0.376]	1.883	[0.49]
Required	1.999	[0.375]	2.337	[0.334]	1.797	[0.399]

NOTE: Mean [SD], In seconds.

3.3.1.2 New Items

For new items, accuracy was high with a correct rejection rate of 0.809 (SD=0.170). Reaction times for correct rejections was 1.587 seconds (SD=0.358) and false alarms was 2.278 seconds (SD=0.497). Two participants did not have any false alarms. A t-test confirmed that the correct rejections were significantly faster than the false alarms [t(22)=-5.737,p<0.001]. Additionally, I found a greater proportion of high confidence responses for correct rejections (Mean =0.743, SD=0.209) than false alarms (Mean =0.191, SD=0.258) [t(22) = 8.243, p < 0.001].

3.3.2 Post-retrieval Neural Activity

3.3.2.1 Alpha and beta desynchronization during successful context memory retrieval

During the retrieval task, I predicted greater theta synchronization and greater alpha/beta desynchronization for invalid compared to valid trials.

Across valid and invalid trials, the results of the spatiotemporal cluster analysis revealed significantly greater desynchronization in the alpha and beta frequency bands, as see in Figure 12. For context hits vs context miss trials. In the alpha band a posterior cluster of 22 electrodes between 0.75 and 1.15 seconds post-stimulus was found across both valid and invalid conditions [t(24)=-4.172,p=0.001], and follow-up analyses found this with significant in the valid [t(24)=-3.668,p=0.003], and marginally in the invalid [t(24)=-1.653,p=0.104] conditions, although the conditions were not significantly different from each other [t(24)=-0.682,p=0.482]. In the beta band a cluster across 17 frontal central electrodes between 0.65 and 1.3 seconds post-stimulus, was found in both conditions [t(24)=-3.730,p=0.002], and follow up analyses revealed it was reliable in both valid [t(24)=-2.650,p=0.026], and invalid [-3.045,p=0.002] conditions. In addition, this beta cluster did not differ between valid and invalid conditions [t(24)=1.082,p=0.288].

For valid trials only, a spatiotemporal cluster analysis found less beta desynchronization for context hits compared to misses in 22 central electrodes between 2.6 and 3 seconds post-stimulus [t(24)=3.983,p=0.003], see Figure 12. The same cluster was not reliable for invalid trials [t(24)=-0.007,p=0.967], and the difference was greater for valid compared to invalid trials [t(24)=2.793,p=0.007]. Given that invalid incorrect context memory responses contain lures (the cued scene), I reran the identified invalid clusters with non-lure context misses. One participant was removed for having to few non-lure misses. For the alpha cluster, the invalid context memory contrast remained marginally significant [t(23)=-1.979, p=0.065], and did not differ from the valid context memory contrast

[t(23)=0.588, p=0.583]. For the early beta cluster, the invalid context memory contrast was still significant [t(23)=-2.992,p=0.006], and was not significantly different from the valid context memory contrast [t(23)=1.661,p=0.109]. For the late beta cluster, the invalid context memory contrast was not reliable [t(23)=-0.518, p=0.615], and the invalid context memory contrast was reliably smaller than the valid context memory contrast [t(23)=3.224, p=0.001]. Follow-up correlations between the late beta cluster power difference and reaction time differences between context hits and context misses was not significant for either valid or invalid conditions [absolute r < 0.27, p > 0.19].

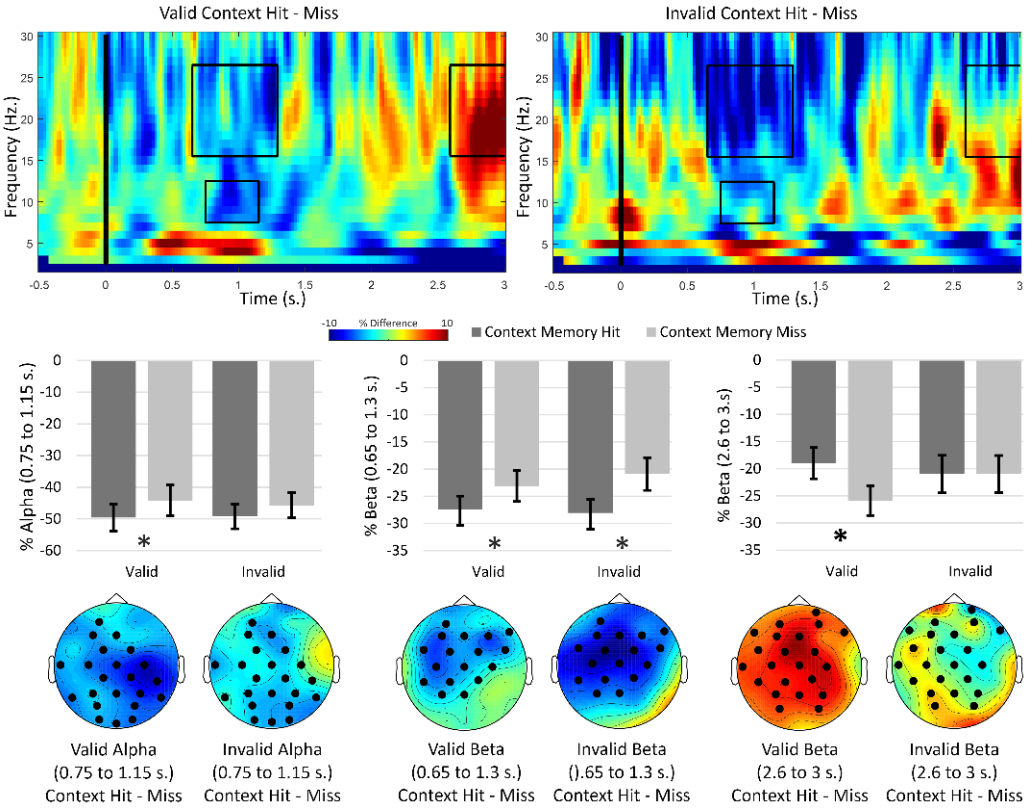

Figure 11: Error bars = 1 SEM. '*' = p < 0.05, cluster corrected. Heat maps are comprised of the intersecting electrodes found in the alpha and beta clusters. Bar charts and topographic maps represent the identified cluster electrodes (highlighted).

3.3.2.2 Theta and alpha negatively correlate with invalid context memory performance

For invalid trials only, the results from a spatiotemporal cluster analysis revealed theta and alpha power was negatively related to successfully context memory retrieval across frontal and central electrodes, see Figures 12 and 13.

Starting from item onset to 0.5 seconds a cluster of 25 electrodes with the theta frequency band was found that negatively correlated with the proportion of correct context memory judgements [r(23)=-0.576, p=0.003]. This early cluster was not significant for valid trials [r(23)=0.205, p=0.325], and the correlation coefficients significantly differed from each other [Fisher's p=0.004]. In a subsequent cluster of 20 frontocentral electrodes between 0.9 and 2 seconds theta power negatively correlated with the proportion of correct context memory judgements [r(23)=-0.644, p=0.001]. This cluster was not significant for valid trials [r(23)=0.236, p=0.256], and the correlation coefficients significantly differed from each other [Fisher's p< 0.001] , see Figure 12.

Finally, alpha power across 17 frontal electrodes between 1.4 and 1.8 seconds post-stimulus negatively correlated with the proportion of correct context memory judgements [r(23)=-0.59, p=0.002], the same relationship was not found for valid trials [r(23)=-0.145, p=0.49], and the correlation coefficients marginally differed from each other [Fisher's p= 0.078], see Figure 13.

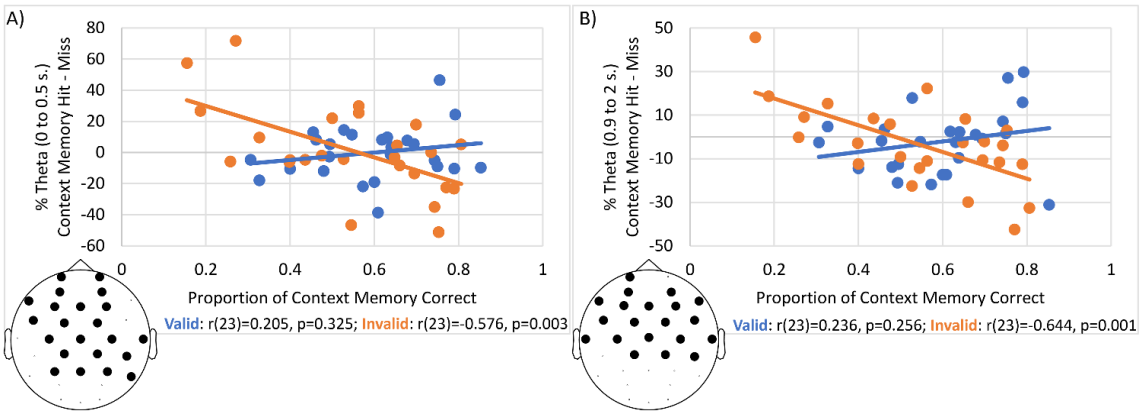

Figure 12: Correlations between the theta context memory contrast at retrieval and context memory performance. A) Correlation cluster was across 25 electrodes from 0 to 0.5 seconds. B) Correlation cluster was across 20 electrodes from 0.9 to 2 seconds.

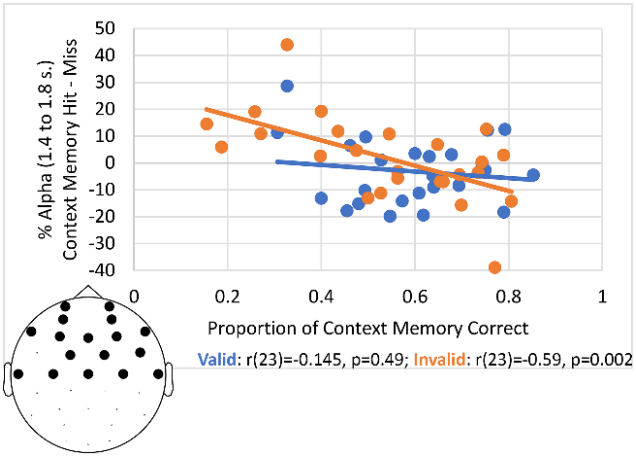

Figure 13: Correlation between the alpha context memory contrast at retrieval and context memory performance. The correlation cluster was across 17 electrodes from 1.4 to 1.8 seconds.

3.3.3 Summary

At retrieval, I did not find greater theta synchronization for successful context hits vs misses, although I may not have had enough power to reliably detect it as visual inspection of the heat maps in Figure 10 suggest this effect exists. Consistent with previous research (for review: Klimesch, 1999; Klimesch et al., 2007) I found greater widespread

alpha and beta desynchronization for successful context memory retrieval in both valid and invalid conditions, which possibly reflects the successful reactivation of the correctly retrieved scene image. I also found greater beta desynchronization for valid context misses than hits very late in the epoch. This late time period corresponds well to the timing of the confidence question. While the onset of the confidence question varied in response to the reaction time of the first question, the reliable onset of the effect is 0.3 to 0.6 seconds after the average reaction times for correct and incorrect context memory judgments, respectively. Follow-up analyses found these effects were not driven solely from the mixture of lures and non-lures in the invalid context memory contrast.

Correlations between EEG power and context memory performance were only found for invalid trials in the theta and alpha frequency bands. Less theta power was correlated with higher context memory for invalid trials. Previous research suggests that mid frontal theta power modulates with the number of retrieved associations (Khader & Rösler, 2011) and working memory load (Gevins, Smith, McEvoy, & Yu, 1997; Jensen & Tesche, 2002). If the invalid cued scene was encoded or interfered with the correct item-scene pairing, then increased theta power may reflect the retrieval of both the paired and invalid lure scene. Therefore, less theta power may reflect the retrieval of a smaller amount of distracting information. I also found alpha power correlated with successful invalid context memory performance. Greater decreases in alpha power may reflect the successful retrieval of the correct scene (Khader & Rosler, 2011), although if this alpha desynchronization was only related to the successful retrieval of the context scene it is surprising that I did not find the same relationship with valid context memory performance. Visual inspection of the scatter plot suggests that less alpha power for worse context

memory performance may be driving this relationship. This would be consistent with studies that find alpha synchronization during the inhibition of distracting information or interference resolution (for review: Klimesch, 2012), which may be required in order to overcoming the invalid lure scene.

3.4 Additional Results and Data

Additional behavioral analyses that include the required trials, and EEG item memory can be found in Appendix A. While there were not enough item misses to assess subsequent memory effects at encoding in the EEG, I contrasted correct item memory for valid, invalid, and required with correct item memory for neutral trials. While not a true subsequent memory contrast, it does highlight how context expectation influences successful item encoding compared to a non-expectation condition. Item memory at retrieval was assessed with the old-new contrast.

Confident judgements were included at retrieval, but confidence was not part of the EEG hypotheses. I reran the univariate EEG analyses including high confident context memory vs context misses (all confidence levels), and these can be found in Appendix B. There were not enough trials to do a high confidence only contrast, but this contrast should be less effected by uncertainty within the context hits.

Finally, Appendix C includes the results from the questionnaires, and Appendix D includes full tables of classification accuracy from the MVPA analyses.

CHAPTER 4. DISCUSSION

Given the accumulating evidence that preparatory processes are part of successful encoding (for review: Cohen et al., 2015; Hanslmayr & Staudigl, 2014; Otten et al., 2006), I investigated how expectation influences context memory by manipulating the validity of a prestimulus context cue at encoding. For each encoding trial, the participant made likelihood judgements about the presence of an item in one of four context scenes (e.g. forest, city, house, office). Preceding each judgement, a context or neutral cue was provided. When a neutral cue was provided, participants did not know which of the four scenes would be paired with the item. When a context cue was provided, it was either valid, invalid, or required. For valid cues, the context cue matched the scene in the item-scene association task. For invalid cues the context cue did not match the presented scene and participants needed to ignore or inhibit the preparatory processes elicited by scene expectation. The required cue condition presented a random color patch instead of a scene, thus, the item-scene relationship needed to be assessed based upon the scene indicated by the cue. Since participants were unaware about the validity of the cue until stimulus presentation, the effect of preparation on context memory performance could be evaluated without trial or stimulus type confounds. Overall, I found behavioral and neural evidence that a valid cue facilitated context memory performance and an invalid cue interfered with context memory performance.

4.1 Behavioral results are consistent with studies of preparatory attention

The behavioral findings are in line with previous studies manipulating attentional orienting (for review: Petersen & Posner, 2012; Posner, 1980). I found valid trials were

faster than neutral trials and invalid trials at encoding, regardless of memory performance, which is consistent with research on visual object recognition (for review: Bar, 2003; Logothetis & Sheinberg, 1996), and memory guided-attention to target locations within scene images (Stokes, Atherton, Patai, & Nobre, 2012; Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006). The same pattern was found for context memory, higher performance for valid than neutral or invalid trials. The faster reaction times across all memory performance conditions suggest that a valid cue facilitated scene recognition and processing, but the benefit to memory encoding is likely due additional processes.

An inhibitory control process may partially explain the higher performance found for valid trials. Successful inhibitory control has been linked to reducing the influence of distracting information and increasing working memory performance (Hasher, Lustig, & Zacks, 2007). For valid trials, the engagement of beneficial trial specific processes (i.e. expected context scene) as well as the disengagement of non-trial related processes could have facilitated performance. For invalid trials, these same processes could have led to the engagement of non-beneficial trial specific processes (i.e. invalid lure scene), and the disengagement of trial related and unrelated processes (e.g. other scenes). Inhibitory control may also influence performance by orienting the participant to the task and reducing non-task related thoughts (e.g. lunch). I found neutral and invalid trials were similar across overall reaction times and context memory performance, while the proportion of neutral high confident context responses was similar to the valid condition. This suggests that the utilization of the invalid lure was more likely to interfere with the quality of the ensuing memory representation, than the binding between the correct context and item. Unfortunately, expectation during neutral trials is speculative and future studies

comparing task relevant (e.g. context) and task irrelevant (e.g. random words; articulatory suppression) preparation may help illuminate the influence of non-task specific preparation on successful memory encoding.

Category expectation has been shown to improve detection and shift neural baselines during recognition tasks (Puri et al., 2009). When these recognition tasks mix exemplar with general category expectation, the valid exemplar expectation shows greater improvements than valid category expectation. In contrast, both invalid exemplar and invalid category expectation impair performance (Puri & Wojciulik, 2008). The current paradigm used all scene images; therefore, all context cues could be considered within category. Subsequent research using different categories of context images may find greater invalid cuing costs, compared to neutral.

4.2 Preparation during encoding directly influences successful encoding

4.2.1 Alpha power correlates with successful valid context memory

I found greater prestimulus alpha desynchronization starting 0.7 seconds before stimulus onset reflected higher context memory performance for trials with a valid cue. The same relationship was not found for invalid context memory. This timing is consistent with the engagement of attentional processes related to temporal expectation (Rohenkohl & Nobre, 2011; Samaha, Bauer, Cimaroli, & Postle, 2015; Wilsch, Henry, Herrmann, Maess, & Obleser, 2014; Zanto et al., 2011), and preparatory engagement of the domain-specific cortical areas (for review: Driver & Frith, 2000; Luck, Chelazzi, Hillyard, & Desimone, 1997). Fluctuations in alpha power are thought to reflect "functional inhibition" where increases may reflect the inhibition to task-irrelevant brain regions (for review:

Jensen & Mazaheri, 2010) or information (for review: Klimesch, 2012), and decreases are related to stimulus processing and the active engagement of task-relevant regions (Hanslmayr et al., 2012; Jensen, Bonnefond, & VanRullen, 2012; Lange, Oostenveld, & Fries, 2013). In other words, changes in alpha power may reflect the mechanism of action in recruiting or quieting brain regions. For example, transcranial magnetic stimulation preceding target identification over task relevant regions (FEF, right IPS) correlates with decreases in both prestimulus parieto-occipital alpha desynchronization and subsequent target detection (Capotosto, Babiloni, Romani, & Corbetta, 2009). While many studies have investigated alpha power in response to an external instruction (e.g. detection, spatial attention, task engagement, temporal expectation), long-term memory can also bias alpha power to the engagement of memory predicated orientations (Stokes et al., 2012). Thus, prestimulus alpha desynchronization for valid trials may reflect the activation of scene specific regions that facilitated detection. But, alpha power did not correlate with overall reaction times suggesting that improved scene detection was not the sole contributor to the improved context memory found in the valid condition.

Alpha desynchronization is also common in memory tasks and thought to reflect the processing or retrieval of specific features (Hanslmayr, Staresina, & Bowman, 2016; Hanslmayr & Staudigl, 2014; Hanslmayr et al., 2012; Khader & Rösler, 2011; Klimesch et al., 2007; Waldhauser et al., 2012), such as the amount or type of information retrieved (Khader & Rosler, 2011; Waldhauser, Braun, & Hanslmayr, 2016). Across all conditions, the encoding task required the processing of a specific scene with an unknown item and evaluating the relationship between them. Changes in alpha power are found for a wide variety to tasks involving attention (Klimesch, 1999, 2012; Klimesch, Doppelmayr,

Pachinger, & Russegger, 1997; Klimesch et al., 2007; Posthuma, Neale, Boomsma, & de Geus, 2001), and in the current study, likely reflect a combination of attentional orienting and scene retrieval. I can speculate that attentional orienting should have improve performance across all conditions, as inhibiting task unrelated thoughts should generally improve performance. But, the retrieval of specific scene details should specifically benefit valid trials. Although, some research with detection and recognition paradigms has shown that invalid within category cues can still be beneficial, while invalid across category cues are detrimental (Puri & Wojciulik, 2008).

Perhaps future research that utilizes separate categories of context memory associates (e.g. faces and scenes), capitalizes on the lateralized alpha activity found in spatial cuing paradigms, or uses more sensitive imaging techniques will be able to test directly for both orienting and retrieval contributions during preparation. Unfortunately, there was not enough trials to investigate neutral or required context memory. Future research that includes enough required trials and neutral trials may be able to discriminate between conditions were context memory is completely dependent on the context cue, and conditions were the cue provides temporal expectancy without a specific scene retrieval process, respectively.

4.2.2 Successful cue discrimination supports valid and interferes with invalid context memory conditions

I hypothesized that reactivation of the cued scene during the cue – stimulus interval would benefit valid and interfere with invalid context memory performance. Previous research has found that successful cortical reinstatement is related to retrieval performance

(Gordon, Rissman, Kiani, & Wagner, 2014; Johnson et al., 2009; Kuhl, Rissman, Chun, & Wagner, 2011; Kuhl et al., 2012; Manning et al., 2011; Morton et al., 2012; Polyn et al., 2005), and this reactivation can impair memory performance when the reactivated elements compete with or do not support the retrieval criterion (Bramão & Johansson, 2018). In the current paradigm, I was not able to find specific evidence of scene image reactivation in response to the visual cue at encoding but did find that the discriminability of the cue was related to memory performance.

Classification accuracy within frontal alpha power was positively correlated with valid context memory performance and with the likelihood of selecting the invalid lure scene at retrieval. Given the alpha frequency band's role in the controlled access to information (for review:Klimesch, 2012), the frontal alpha effect could reflect accessing the cued scene from long-term memory or applying top-down activation to the relevant processes engaged in facilitating detection and recognition of the expect scene (Haegens, Händel, & Jensen, 2011). Another possibility is that participants with higher classification accuracy for discriminating between the cue types were more engaged with the task. While this could be contributing to successful valid context memory, I would have expected that being more engaged would also benefit invalid trials if the engagement did not bias preparation based on the cue information.

Interestingly for invalid trials only, I found that classification accuracy across all electrodes and frequency bands negatively correlated with memory performance or put another way greater widespread classification accuracy positively correlated with selecting an incorrect scene (lure and non-lure). This feature set included the theta and beta frequency bands as well as posterior electrodes, which would be expected to play a greater

role in retrieving the cued scene. Thus, one possibility is that higher levels of reactivation may have been strongly related to the ability to recall the lure scene as a lure while not being able to retrieve the originally presented image. For valid trials, fully retrieving the scene may not have provided an added benefit greater than biasing stimulus detection regions to a preferred scene.

4.2.3 No Preparatory theta power related to context memory

Previous research has found increases in prestimulus theta power are related to successful memory encoding (Fell et al., 2011; Gruber et al., 2013; Guderian et al., 2009; Merkow, Burke, Stein, & Kahana, 2014), although the manifestation of these effects varies between studies and task characteristics. Changes in prestimulus theta power during encoding are thought to reflect the activation of contextual information (Fell et al., 2011; Guderian et al., 2009) that aids in building the subsequent memory representation. If theta reflects the activation of contextual information during the cue-stimulus interval, then I expected the activation of inaccurate information (i.e. invalid lure scene) would result in worse memory performance. Studies that change contextual information between encoding and retrieval have shown negative theta effects for the changed condition (Fell et al., 2011; Staudigl & Hanslmayr, 2013). In the current paradigm prestimulus cues were used to activate contextual information for one of the four specific scene images. Thus, I had predicted that prestimulus theta power would positively correlate with successful valid context memory performance, and negatively correlate with successful invalid context memory performance. Unfortunately, I did not find a relationship between prestimulus theta power and context memory performance for either the valid or invalid conditions.

In nearly all studies of preparation with episodic memory paradigms, a prestimulus cue provided the participants with trial related information in advance of the upcoming stimulus, and therefore the meaning of the cue must be retrieved from memory. During retrieval greater theta synchronization is commonly found successful compared to unsuccessful retrieval (Addante et al., 2011; Gruber, Tsivilis, Giabbiconi, & Muller, 2008; Hanslmayr & Staudigl, 2014; Hanslmayr, Staudigl, Aslan, & Bauml, 2010; Hsieh & Ranganath, 2014; Jacobs et al., 2006; Khader & Rosler, 2011; Klimesch, Doppelmayr, Yonelinas, Kroll, Lazzara, Rohm, et al., 2001; Nyhus & Curran, 2010; Osipova et al., 2006; Staudigl et al., 2010), and is greatest during the accurate recovery of contextual information (Addante et al., 2011; James, Strunk, Arndt, & Duarte, 2016; Khader & Rösler, 2011; Osipova et al., 2006). Since there was not a direct behavioral measure of cue retrieval, I cannot tease apart performance on specific cue retrieval trials vs non-retrieval trials for the valid and invalid conditions. Given that average reaction times at encoding were shorter than the minimum item – scene presentation time, the two second presentation time may have mitigated the influence of cue validity on a large proportion of trials in the valid and invalid conditions. Future studies that include greater proportions of required or neutral trials may be better suited to directly investigate when retrieval of the cued scene is paramount for successful context memory encoding and neutral trials where specific scenes are unlikely to be retrieved. In addition, decreasing the item – scene presentation time may increase the validity effect by increasing the reliance on cue information during stimulus presentation.

4.3 Retrieval induced facilitation and interference on post-stimulus encoding

4.3.1 Posterior beta desynchronization reflects successful invalid context memory encoding

Greater beta desynchronization was found for invalid context memory hits compared to context misses, while there was not a context memory difference for the valid trials. Previous studies have linked greater beta desynchronization during successful encoding to indexing the specific neural correlates of engaging with the task demands (e.g. stimulus and task), which in turn should increase the probability of successful encoding (Hanslmayr et al., 2012). Desynchronization within the beta band may correlate with increases in fMRI activity within task relevant regions (Zumer, Brookes, Stevenson, Francis, & Morris, 2010). For example, the encoding of verbal materials during encoding has found that better memory performance correlated with greater beta desynchronization over left frontal electrodes and increased fMRI activity in the left inferior-frontal gyrus (Hanslmayr et al., 2011). For semantic encoding tasks, changes in left frontal beta power are thought to reflect the semantic aspects of the orienting task that contribute to memory formation (Hanslmayr et al., 2009; Hanslmayr & Staudigl, 2014; Hanslmayr et al., 2011). An important difference between memory encoding studies that link left beta power with successful encoding and the current encoding paradigm is the use of an associative orienting task between an item and scene image. Processing visual information (e.g. pictures) has been shown to increase desynchronization within visual processing and perception regions (Maratos, Anderson, Hillebrand, Singh, & Barnes, 2007; Singh, 2012), which is in line with the increase in beta desynchronization over posterior and occipital electrodes for invalid contexts hits.

Given that successfully scene processing should benefit all the conditions, it is surprising that I did not find context memory related beta desensitization for valid trials. One possibility is that the scene cue reduced the need for stimulus processing or changed the threshold needed for processing the scene stimulus. Another possibility is that the increased beta desynchronization found for invalid context hits is not reflecting stimulus processing but cognitive processes involved in updating the memory representation, cognitive state, or continued processing of the successful switch away from the invalid lure scene (Engel & Fries, 2010). Perhaps future research that utilizes neutral context memory would be able to resolve these options as neutral trials do not allow for specific scene preparation, and therefore should solely rely on stimulus driven processing without a violation of expectation.

Finally, beta desynchronization is most consistently tied to motor functions (Pfurtscheller, Stancak Jr, & Neuper, 1996) and I found that reaction times were on average faster for valid compared to invalid trials. But, validity and memory performance did not interact, and correlations between beta power and reaction times failed to find significant relationships. Thus, it is unlikely that the beta effect was related to the motor response.

4.3.2 Successful scene classification supported both valid and invalid context memory performance

As predicted, during the item – scene stimulus presentation I found that classifier evidence was higher and above chance for trials with a valid cue, and at chance for trails with an invalid cue. One way in which expectation is thought to enhance perception is through sharpening the sensory representation by biasing activity within the visual cortex

(Kok, Jehee, & De Lange, 2012). This expectation may have facilitated encoding the item – scene pairing for valid trials as classifier evidence within the occipital cluster positively correlated with valid context memory performance. For invalid trials, the classifier was less robust and wasn't above chance suggesting that the expected perceptual activation intermixed with the presented perceptual details which obfuscated the memory representation. This is in-line with previous fMRI research that finds coactivation of target and competing associations in the visual cortex during memory retrieval, and that the greater interference from the competing association reduces memory performance (Kuhl et al., 2011).

Interestingly, I found that classification accuracy within parietal theta positively correlated with invalid context memory performance and with a lower probability of incorrectly selecting the invalid lure scene at retrieval. Fluctuations in theta power are found during interference resolution (Hanslmayr et al., 2010), as well as successful encoding and retrieval (Hsieh & Ranganath, 2014; Khader, Jost, Ranganath, & Rosler, 2010; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010). Given that theta power is associated with binding together contextual elements during encoding and reactivating those elements at retrieval, one possibility is that participants with less interference during the item- scene pairing where more likely to have demonstratable pattern differences reflecting the activation of the specific scenes.

In addition, classification accuracy for the beta power within both parietal and occipital electrode clusters positively correlated with the context memory validity effect. One possibility is this reflects a difference in the number of trials that went into the classifier accuracy measure. There were more valid trials contributing to overall

classification accuracy than invalid trials, and above chance performance was only found for the valid trials. For valid trials, if expectation successfully sharped then representation, as previously suggested, then this might represent the benefit of valid cues, and the higher context memory performance. Future research that investigates the valid vs neutral and the invalid vs neutral contrasts may be able to determine if post-stimulus classification accuracy is reflecting the benefit of a valid cue, the interference of the invalid cue, or both.

4.3.3 Post-stimulus theta power did not support successful context memory encoding

I predicted that successful context memory would be associated with greater post-stimulus theta for invalid trials compared to valid trials. Neither condition produced reliable differences between successful and unsuccessful context memory encoding. This is surprising considering the plethora of previous memory encoding studies that find memory related theta fluctuations which onset around 0.3 seconds post-stimulus and are generally attributed to successful encoding or binding of source details (Hanslmayr et al., 2009; Klimesch, Doppelmayr, Schimke, & Ripper, 1997; Mölle, Marshall, Fehm, & Born, 2002; Osipova et al., 2006; Sederberg et al., 2003; Staudigl & Hanslmayr, 2013; Summerfield & Mangels, 2005). A unique aspect of the current encoding paradigm is the use of trial specific associative context cues instead of task informational cues (e.g. stimulus modality, orienting task, value). In the previous research, processing the contextual elements happened in response to the stimulus as the exact associates are generally not know ahead of time. As such, increases in theta power related to memory performance would be expected as all tested associations are presented at the same time. In other words, stronger associations at encoding commonly lead to better memory performance for the associations.

In the current task, for valid trials the context image could have been retrieved ahead of the item – scene pairing, which may have mitigated the expected post-stimulus increase in theta synchronization. For invalid trials, interference related increases in theta may reflect trials with a higher probability of incorrectly selecting the context scene at retrieval. Thus, context misses could be a combination of high interference trials, low associative strength trials, and trials with the successful retrieval of an incorrect scene. Perhaps in the current design, increases in post-stimulus encoding theta would be reflected in an item memory contrast where forgotten items should lack any contextual details.

I specifically predicted greater post-stimulus theta power for invalid compared valid trials on the basis that invalid trials may contain greater associative links (i.e. invalid lure scene), but also because changes in theta power are found during conflict and error processing (such as task switching). As previously discussed, theta power has been shown to increase with working memory load (Jensen & Tesche, 2002) and the amount of associative links or contextual details during retrieval (Khader & Rosler, 2011). While the total number of associative links could be greater for invalid compared to valid trials, the total amount of goal-oriented information would have been similar. Instead of holding two scenes in working memory for invalid trials, the active working memory scene needed to be updated. Given the highly similar context scenes, updating working memory with the same load size may not appreciably change the amount of theta power. Future studies that use associates from different categories types might find transitional periods related to switching the associative links to different neural regions, which may be reflected as separable topographical patterns. Additionally, changes in theta power might not be in overall power but instead in the specific frequency within theta as the specific frequency

within the theta band has also been shown to modulate with memory load (Jensen and Lisman, 1998).

Early increases (under 0.5 seconds) in theta power have been found in cognitive control tasks during interference (e.g. Go-No-Go, Flanker, Simon) (Nigbur, Ivanova, & Stürmer, 2011; Yamanaka & Yamamoto, 2010), task switching (Sauseng et al., 2006), and with violations of an expectation or rule (Tzur & Berger, 2007). These theta changes are can be detected over frontal electrodes, and source localization suggests this interference related theta power is reflected by increased power in and coherence between the anterior cingulate cortex (ACC) and lateral prefrontal cortex (Cavanagh, Cohen, & Allen, 2009; Hanslmayr et al., 2008; Luu, Tucker, & Makeig, 2004; Trujillo & Allen, 2007; Yordanova, Falkenstein, Hohnsbein, & Kolev, 2004). Interference in the current paradigm was at the level of an internal image representation and not linked to a specific response outcome or taskset, and likely did not produce enough interference to be detectable. Previous research has shown that theta related interference resolution may be maximal within the region where the interfering information is processed (Nigbur et al., 2011), and the within category (i.e. context scenes) regions were already engaged in the retrieval and maintenance of a scene. Finally, interference from the invalid lure scene may have resulted in a combination of context misses and item misses, thus it was not strong enough to detect. Alternatively, early evoked theta is found during stimulus processing, which may have also been greater than the contribution from error-related processing.

Required trials might be a good indicator memory related theta power, as successful context memory is dependent on the retrieval of the cued scene (regardless of when the retrieval happened). Thus, we might expect greater theta power at encoding due to the

retrieval and maintenance of the context scene, whereas the other conditions do not require working memory maintenance of the context scene. Neutral trials with no scene specific preparation may also be informative as the associative links are all engaged at the time of the stimulus. Future studies that include enough context correct and incorrect trials within the required and neutral conditions may help speak to these possibilities. Additionally, varying the concurrent memory load, may help to investigate if both the invalid lure and correct scene have the same theta response as holding two scenes in working memory.

4.3.4 Post-stimulus alpha power did not support successful context memory encoding

I had predicted greater alpha desynchronization for invalid compared to valid trials but did not find context memory related alpha desynchronization for either valid or invalid trials. This predication was based on the same logic that greater theta synchronization would be found; greater cognitive demands on invalid trials due to processing the additional scene and updating to a new scene for the encoding association task.

Fluctuations in alpha power during encoding is thought to reflect the successful recruitment of regions related to processing stimulus features and executing the task demands, as well as the recruitment of non-specific attentional processes (Klimesch, 1999, 2012; Klimesch, Doppelmayr, Pachinger, & Russegger, 1997; Klimesch et al., 2007). As previously discussed, alpha may facilitate cognition through inhibitory control were decreases reflect the engagement of regions involved in goal relevant processes (e.g. disinhibition), while increases may reflect the disengagement of uninvolved regions (Jensen & Mazaheri, 2010). Increases in alpha power are also found when information needs to be protected or isolated from interference, for example during the retention

interval of working memory tasks (Jensen, Gelfand, Kounios, & Lisman, 2002; Klimesch, 2012; Klimesch et al., 2007). Separating the to-be-remembered information from interfering input would aid in reducing the possibility of distraction and increase the likelihood of preserving the information (Ranganath, Cohen, & Brozinsky, 2005). Alpha power may reflect the mechanism in which regions are functionally engaged or disengaged based on processing demands, and thus decreases may indicate a release from inhibition in relevant areas, and increases may reflect isolation of regions either not involved in the task demands or those that need protection from interference. Measurement of alpha under these conditions can be tricky, as increases in alpha have been shown to positively modulate with memory load in simple working memory tasks (Jensen et al., 2002), but may reverse when tasks demands are high (Gevins et al., 1997). In other words, memory related increases may not overcome task related decreases in the measured signal. Future research with explicit changes in working memory load may shine a light on these possibilities.

4.4 Retrieval

For context memory retrieval I predicted increased theta synchronization and greater alpha / beta desynchronization for context memory hits compared to context memory misses, and the context memory contrast would be greater for invalid compared to valid trials. As previously discussed, theta synchronization during episodic memory retrieval is thought to reflect higher order memory control processes (Hanslmayr et al., 2010; Staudigl et al., 2010) and been found to modulate with the amount of information retrieved (Khader & Rösler, 2011) as well as working memory load (Jensen & Tesche, 2002; Mecklinger, Kramer, & Strayer, 1992). For the alpha and beta frequency bands desynchronization has been shown to modulate with the type and amount of information retrieved (Burgess &

Gruzelier, 2000; Khader & Rösler, 2011; Waldhauser et al., 2016; Waldhauser et al., 2012) as well as correlate with context memory performance across participants (Strunk et al., 2017). In addition, larger effects have been found in all frequency bands during interference and as a function of memory load (Khader & Rösler, 2011; Lundqvist, Herman, & Lansner, 2011; Staudigl et al., 2010; Waldhauser et al., 2012). Overall, I found alpha and beta desynchronization across valid and invalid trials during retrieval, greater beta desynchronization during the confidence question for valid context misses, and negative correlations between the proportions of invalid context memory hits and the context memory contrast within the alpha and theta frequency bands.

Consistent with previous studies suggesting alpha and beta desynchronization during memory retrieval are related to reactivation of the retrieved information (Burgess & Gruzelier, 2000; Khader & Rösler, 2011; Waldhauser et al., 2012), I found greater desynchronization in both alpha and beta frequency bands for context memory hits compared to misses across both valid and invalid trials between 0.7 and 1.3 seconds after stimulus onset.

For invalid trials only, I found negative correlations between the proportions of invalid context memory hits and the context memory contrast within the theta and alpha frequency bands. Previous research has found greater mid-frontal theta power for task conditions with interference compared to non-interference conditions during response conflict paradigms (Cavanagh et al., 2009; Hanslmayr et al., 2008) as well as paradigms with competitive retrieval (Hanslmayr et al., 2010; Waldhauser et al., 2012). In Waldhouser et al. (2012), this interference related increase in theta was found in two similar time windows as the current dissertation (early and late). While I did not explicitly predict two

different times windows, one may speculate that the early onset time window may reflect detection of interference from the retrieval cue (i.e. item presentation) which would facilitate communication between the anterior cingulate cortex (ACC) and lateral prefrontal cortex (Cavanagh et al., 2009; Hanslmayr et al., 2008; Luu et al., 2004; Trujillo & Allen, 2007; Yordanova et al., 2004) while the second later time window may be more directly related to the retrieval of the associated scene (Duzel, Penny, & Burgess, 2010; Hsieh & Ranganath, 2014; Jacobs et al., 2006; Khader & Rosler, 2011; Klimesch, Doppelmayr, Yonelinas, Kroll, Lazzara, Roehm, et al., 2001; Osipova et al., 2006). Overall, increases in frontal theta power have been associated with interference conditions (Hanslmayr et al., 2010; Waldhauser et al., 2012), and that successful resolution of interference has been shown to reduce theta power (Staudigl et al., 2010), it is likely that successful invalid context memory is related to effective interference resolution as reflected by reduced theta synchronization. Another, non-mutually exclusive possibility is that participants who did not encode the lures at encoding would be expected to have higher memory performance and lower interference related theta synchronization. Future research that utilizes lateralization effects found in spatial memory tasks may be able to identify separable contributions from selecting the appropriate associative information from inhibiting the interfering information (Waldhauser et al., 2012)

Greater alpha desynchronization was also found to correlate with higher invalid context memory performance in a time window that overlaps the late theta time window and follows the alpha / beta context memory effects. One possibility is that greater alpha desynchronization reflects the successful reactivation of the presented scene (Hanslmayr et al., 2016; Hanslmayr et al., 2012; Khader & Rösler, 2011; Waldhauser et al., 2012), and

the overlapping time windows reflect the interplay between higher level memory retrieval processes reflected by theta power with the controlled access to specific sensory details reflected in within the alpha frequency band (Klimesch, 2012; Sauseng et al., 2002).

For valid trials, the greater desynchronization found in the beta band for context misses during the confidence question is hard to interpret. The first retrieval question was on the screen for two to four seconds depending on when the participant responded, and thus the onset of the confidence question was not stable across trials. Perhaps future studies that fix the time period between retrieval and confidence questions, or investigate response related EEG, would be better suited to interpreting the greater desynchronization for valid context misses.

4.5 Decoding the familiarization task

During the familiarization task cue, MVPA across all channels and frequency bands failed to discriminate between the four scene cues. Within the alpha frequency band across frontal electrodes I was able to successfully discriminate between the four scene cues. I was also able to successfully classify the imagine trials above chance within the alpha frequency band in a cluster of two right frontocentral electrodes.

During the familiarization task scene, MVPA across all channels was successfully able to discriminate the presented scenes, and feature selection suggests that all frequencies and channels were contributing to classification success. Visual inspection of the accuracy values would suggest that the posterior electrodes were contributing the most, even though the cluster analysis grouped posterior electrodes into two separate clusters, parietal and occipital. This is in line with previous studies that were able to distinguish between within

category scenes during scene presentation (Bonnici et al., 2012; Johnson & Johnson, 2014). Although, none of the specified features or overall classification were able to successfully decode the imagine trials.

It is possible that there was not enough imagine trials (10 per scene) to reliably capture above chance performance, or that the particular patterns during retrieval of each scene were less robust than during visual presentation. Another possibility is that encoding and retrieval may recruit similar regions and processes, but the activation patterns within them may differ (Kirwan, Ashby, & Nash, 2014), which could lead to indistinguishable topographical patterns in the EEG. While not related to the goal of the study, it is important to note that I was able to reliably classify four scene images with a 32 channel EEG system.

4.6 Limitation and future directions

There are a few notable limitations within this dissertation. First context memory for valid trials was only about 6% higher than invalid trials, and while significant, increasing the valid to invalid trial ratio may have led to a larger performance difference. Another possibility for increasing participant cue use would be to decrease the amount of time the stimulus was on the screen during encoding. Two seconds may have been long enough to overcome some of the invalid cue interference as well as mitigate some of the behavioral advantage of knowing the presented scene ahead of time. Reaction times at encoding were around 0.15 seconds faster for valid compared to invalid trials, but on average all reaction times were under the 2 seconds stimulus presentation time. Reducing scene presentation to less than the average response time may increase reliance on cue information and increase the validity effect. Another possibility would be to associate

ambiguous cues with each scene image, so that descriptive cues are free from previously associated exemplars.

Another limitation is presenting centralized super imposed images during encoding. This was done to reduce lateralization and spatial preparation effects, which could have attenuated the univariate EEG as well as bias the classifier to detect spatial preparation and not scene specific activations. Spatial coding of objects and images has been shown to have robust lateralization effects (Sauseng et al., 2005) which could have been used to assess competition of a competing stimulus location as well increase the sensitive of the classifier. While this would have confounded interpretations about reactivation of specific scenes, we could have still concluded that the use of preparatory information has direct influences on successful memory encoding, and it could have increased our ability to detect interference, interference resolution, and classification. Perhaps future studies that include spatial coding to specific associative images as well as spatial only encoding cues would be able to disassociate spatial preparation from preparatory retrieval of specific imagines.

Given that there were not enough trials to investigate the neural correlates of context memory in neutral trials, it is hard to provide a standard baseline for facilitation within valid trials and interference within invalid trials. Future research that includes enough neutral trials, or possibly a neutral trial control group may help determine which neural signals are directly related to success and failure within this specific task. Required trials would also be an interesting route to investigate because the participant has to rely on the advanced information to make their decision, and the item memory analysis in Appendix A suggests a lot is going on with these trials. Required trials may provide a better measure of the usefulness of preparation than the valid trials, which likely contain a mixture

of trials in which the participant used the preparatory information and trials they did not. Future studies that include different ratios of valid, invalid, neutral, and required trials may help reveal how different aspects of preparation or the failure of preparation contribute to successful encoding.

4.7 Conclusion

In conclusion I found behavioral, univariate, and multivariate evidence that preparation influences successful memory encoding. In addition to supporting the hypothesis that preparation can help and hinder memory encoding, this dissertation adds a number of additional contributions to the literature. First it uses a novel task paradigm that combines an attentional cuing paradigm with an episodic memory paradigm, in order to investigate preparation without task or stimulus confounds. Second, most EEG MVPA studies use large electrode arrays and discriminate images at the category level, while I was able to successfully discriminate between four specific scene images on a 32 channel EEG system. Finally, I provided recommendations for increasing the validity effect in subsequent research to aid in quantifying the role of preparation as well as qualifying the manifestation of preparatory neural activity. Future research manipulating the type of interference, the proportion of trials within each category, and stimulus durations will provide even greater insight into the role of preparation.

APPENDIX A.

A.1 Behavioral Performance: Memory and Reaction Times

Numerical values for memory performance can be found in Table 3. For item memory, a one-way ANOVA with four conditions (valid, invalid, neutral, and required) assessed Pr and found marginal differences between the conditions [$F(3,72)=2.387, p=0.090, \eta p2=0.090, \beta=0.511$]. Follow-up analyses with t-tests found valid Pr was significantly greater than required Pr [$t(24)= 2.665, p = 0.014$]. No other significant Pr differences between conditions were found [absolute t's < 1.535, p's > 0.134]. For context memory, a one-way ANOVA with four conditions (valid, invalid, neutral, and required) assessed the proportion of context correct responses, and the results failed to find significant differences between the conditions [$F(3,72)= 1.677, p= 0. 196, \eta p2= 0.065, \beta=0.344$]. Follow-up analyses with t-tests found the significantly higher context memory for the valid compared to the required condition [$t(24) = 2.294, p = 0.031$]. Neither the invalid or the neutral conditions were significantly different from the required condition [absolute t's < 0.67, p's > 0.5].

For the proportion of high confidence context memory, as seen in Table 5, a one-way ANOVA with four conditions (valid, invalid, neutral, and required) assessed the proportion of high confidence responses within correct context memory judgements and the results indicated a significant difference between the conditions [$F(3,72)=3.143, p=0.040, \eta p2=0.116, \beta=0.644$]. Follow-up t-tests revealed that valid trials had significantly greater high confidence judgements compared to invalid [$t(24)=2.073, p = 0.049$] and required [$t(24)=2.860, p=0.009$] trials, but did not significantly differ from neutral trials

[t(24)=0.245, p=0.809]. The proportion of context correct neutral trials with high confidence were marginally greater than invalid [t(24)=1.944, p=0.064] and required [t(24)=1.995, p=0.057] trials. Finally, the proportion of high confident context correct responses for invalid and required trials did not significantly differ from each other [t(24)=0.476, p=0.639].

Reaction times for encoding can be found in Table 6. One participant was excluded from the ANOVAs due to not having any item misses in the required cue condition. At encoding a 4 Condition (valid, invalid, neutral, and required) x 3 Accuracy (context correct, context incorrect, item miss) ANOVA revealed a significant main effect of condition [F(3,69)=8.228,p=0.001, ηp2=0.263, β=0.941], but not accuracy [F(2,46)=0.765,p=0.451, ηp2=0.032, β=0.160] or a condition by accuracy interaction [F(6,138)=1.501, p=0.220, ηp2=0.061, β=0.391]. Follow-up t-tests found valid trials were significantly faster than invalid [t(24)=-8.998, p<0.001], neutral [t(24)=-3.985, p=0.001], and required [t(24)=-4.115,p<0.001] trials. Invalid, neutral, and required trial reaction times did not significantly differ from each other [t's <1.96, p's > 0.063]. Thus, a valid cue decreased overall reaction times irrespective of subsequent memory performance.

Reaction times for retrieval can be found in Table 7. At retrieval, a 4 Condition (valid, invalid, neutral, and required) x 3 Accuracy (context correct, context incorrect, item miss) ANOVA revealed a significant main effect of accuracy [F(2,46)=24.888, p<0.001, ηp2=0.520, β=1.000], but not condition [F(3,69)=0.537, p=0.619, ηp2=0.023, β=0.142] or a condition by accuracy interaction [F(6,138)=1.168, p=0.330, ηp2=0.048, β=0.325]. Follow-up analyses revealed that context correct, and item misses did not significantly differ from each other [t(24)=1.329, p = 0.196], but context incorrect trials were slower

than context correct [t(24)=5.736,p<0.001] and item misses [t(24)=5.915, p<0.001]. Thus, cue validity during encoding did not significantly influence reaction times at retrieval.

Overall, results from the behavioral analyses with required cue trials found similar memory performance and reaction times to invalid cue trials.

A.2 Item Memory: Encoding EEG

There were not enough item misses to do a true subsequent memory contrast (approximately 15% of each condition). In order to assess differences in correct item memory judgements, I contrasted successful item memory (context hit, and context miss trials) for valid, invalid, and required conditions with the neutral condition. In addition, the inclusion of context hits in the item memory condition, confounds context and item only interpretations. Unfortunately, the limited number of item misses in the required and neutral conditions prohibited a reliable item only assessment. While not a true memory only comparison, it does allow for the assessment of how expectation (valid, invalid, required) influences successful item encoding over a non-context cue expectation baseline (neutral hits), see Figures 15 and 16. No correlations between corrected recognition (Pr) and EEG power were found.

In the theta frequency band, greater post-stimulus synchronization was found for the required hits compared to both the valid and invalid contrasts. The results from spatiotemporal cluster analyses revealed theta synchronization between 2.5 and 4.5 seconds post-cue (0 to 2.5 seconds post-stimulus) was significantly greater across 31 widespread electrodes for the required compared to the valid contrast [t(24)=4.327, p=0.001], and 25 electrodes for the required compared to the invalid contrast [t(24)=4.388,

p=0.001]. Follow-up analyses of the spatiotemporal clusters did not find significant differences between the valid vs invalid contrasts [t's <1.61, p's>0.1].

In the alpha frequency band, less prestimulus desynchronization was found for required hits compared to both valid and invalid hits. The results from spatiotemporal cluster analyses revealed alpha desynchronization between 1.7 and 3 seconds post-cue (-0.8 to 0.5 seconds post-stimulus) was significantly less for required compared to valid trials across 14 posterior electrodes [t(24)= 3.195, p=0.005], which follow-up analyses revealed was also significant between required and invalid hits [t(24)=2.671, p=0.015]. The spatiotemporal cluster did not significantly differ between valid and invalid hits [t(24)=0.493, p=0.624].

In the beta frequency band, greater post-stimulus desynchronization was found for invalid hits compared to valid and required hits. The results from spatiotemporal cluster analyses revealed beta desynchronization between 3.85 and 4.4 seconds post-cue (1.35 to 1.9 seconds post-stimulus) was significantly greater for invalid vs valid hits across 19 left posterior electrodes [t(24)=-3.601, p=0.002], which follow-up analyses revealed was also significant between invalid and required hits [t(24)=-2.640, p=0.017]. The spatiotemporal cluster did not significantly differ between valid and required hits [t(24)=-0.168, p=0.866].

Thus, successful item memory for required trials is characterized by less prestimulus alpha desynchronization and greater post-stimulus theta synchronization compared to valid and invalid hits. To speculate, alpha synchronization during working memory tasks has been shown to reflect working memory maintenance and long-term memory performance (Khader et al., 2010). Given that the encoding task includes a prestimulus period where the

cued scene could be retrieved and held in working memory, the retrieval and maintenance of the scene representation may induce alpha synchronization. But, temporal expectation and external orienting are also reflected by alpha desynchronization (Rohenkohl & Nobre, 2011; Wilsch et al., 2014; Zanto et al., 2011) , thus the total change in measured scalp alpha power would reflect the summation of these processes. The greater amount of wide spread post-stimulus theta synchronization for the required condition may be due to the unique aspects of either combining the to-be-encoded item with an active memory representation or an additive effect of retrieving the scene representation while encoding the item into memory. Future studies aimed at teasing apart theta during concurrent encoding and retrieval may illuminate how internal and external representations are bound together. For example, including a neutral condition that presents a scene label instead of a scene image may help in teasing apart the cognitive processes utilized by the required cue condition.

The greater beta desynchronization found for invalid hits may be due to updating and processing the new scene image. As shown in the context memory analysis, invalid correct context memory was associated with greater beta desynchronization than invalid incorrect context memory, and no differences in beta were found between context memory accuracy in the valid condition. Thus, the beta effect found here likely reflects a context memory effect and not an effect of item memory.

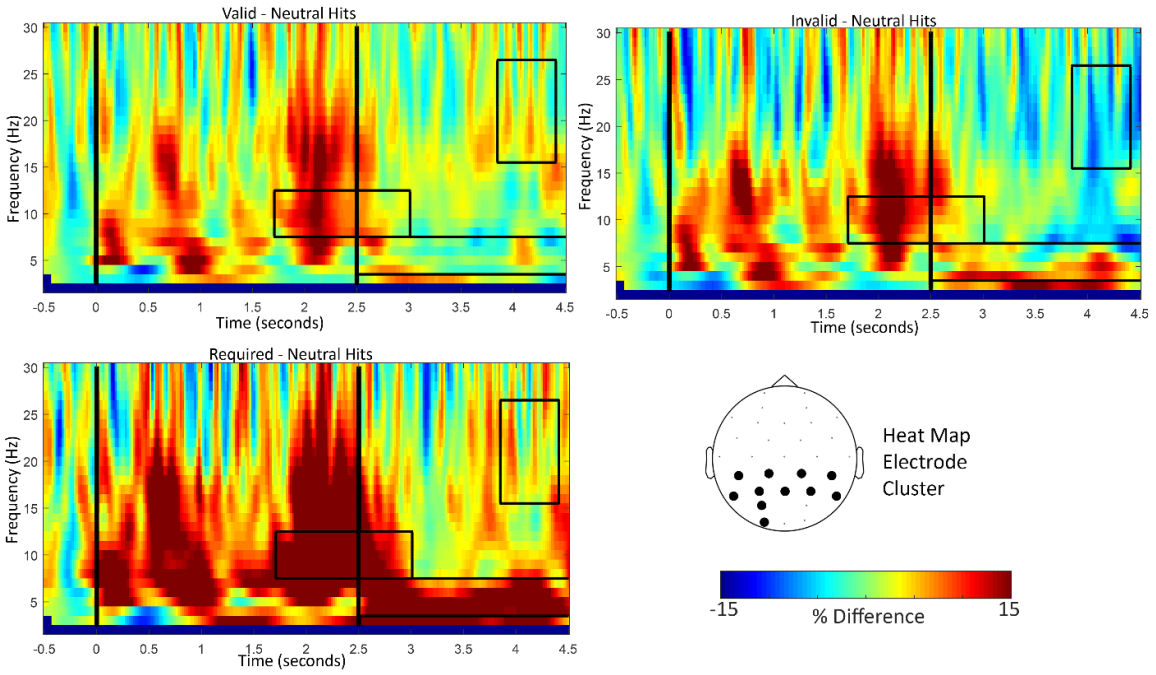

Figure 14: Heat maps are comprised of the intersecting electrodes (highlighted) found in the theta, alpha, and beta clusters. Cue onset = 0 seconds, Stimulus onset = 2.5 seconds

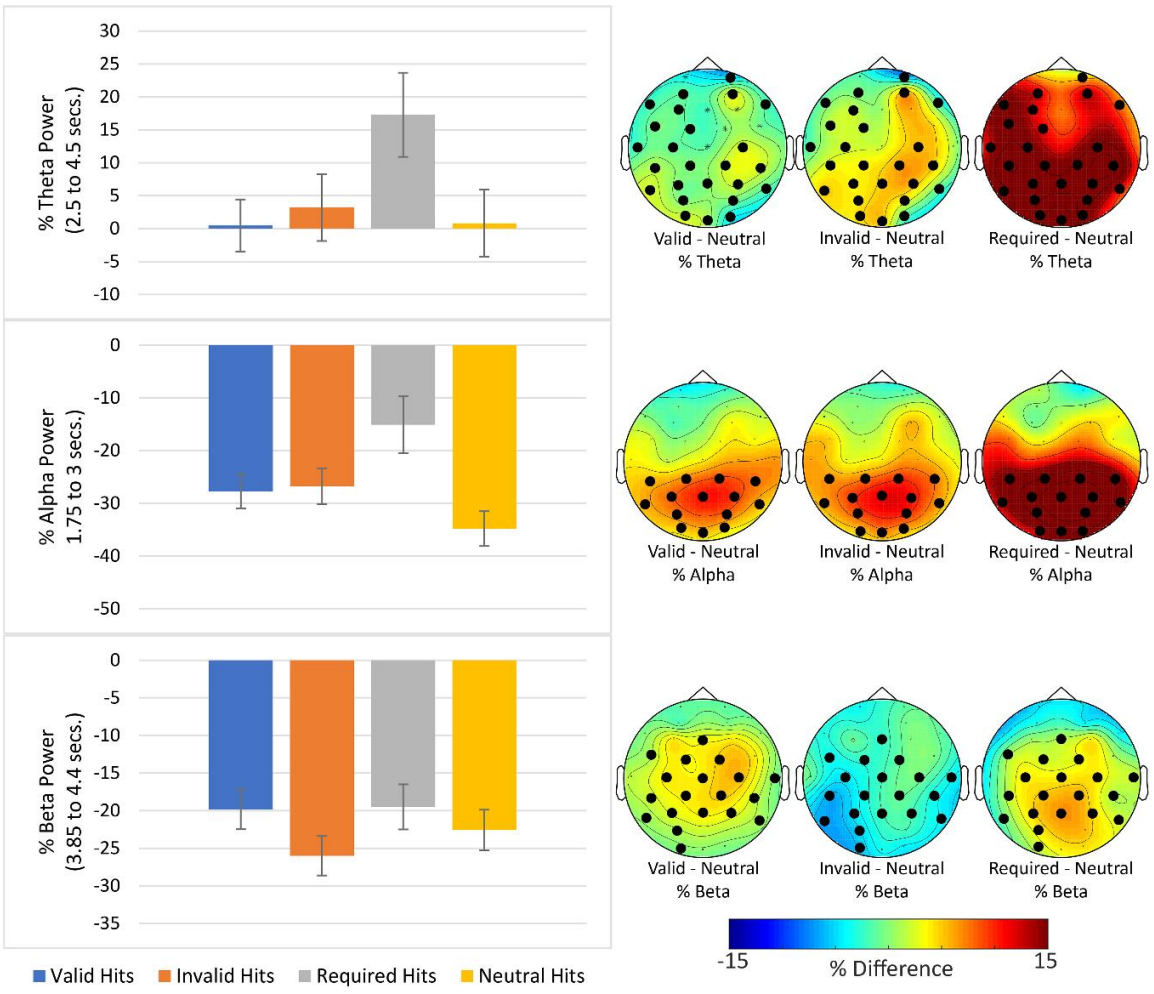

Figure 15: Bar charts and topographic maps represent the identified cluster electrodes (highlighted). Error bars = 1 SEM. All time measurements are from cue onset (stimulus onset = 2.5 seconds)

A.3 Item Memory: Retrieval EEG (Old – New Effects)

Item memory at retrieval was assessed with the old-new effects, see Figure 17 and Figure 18. Cluster analysis did not find correlations between corrected recognition (Pr) and spatiotemporal EEG clusters that correlated with the old-new effect.

The results of cluster analyses found greater alpha desynchronization between 1.8 and 2.25 seconds across 25 electrodes for valid hits compared to correct rejections [t(24)=-

3.216, p=0.002], and across 19 electrodes for invalid item hits compared to correct rejections [t(24)=-3.167, p=0.003], which did not significantly differ from each other [t(24)=0.471, p=0.618]. Follow-up analyses found this spatiotemporal cluster was significant for neutral item hits vs correct rejections [t(24)=-3.167, p=0.003], and did not differ from the valid item hits vs correction rejection contrast [t(24)=-0.485, p=0.627]. The same spatiotemporal cluster was not reliable for required item hits vs correct rejections [t(24)=-1.018, p=0.354], and significantly smaller than the valid old-new contrast [t(24)=2.066,p=0.038]. The results of another cluster analyses found significantly less old-new alpha desynchronization between 0.95 and 2.3 seconds for required compared to the valid condition across 18 frontal electrodes [t(24)=-4.437, p=0.001], and the invalid condition across 12 frontal electrodes [t(24)=-3.134, p=0.002]. Follow-up analyses for this spatiotemporal cluster found it was reliably larger for the neutral condition as well [t(24)=-2.794, p=0.011], and the old-new clusters were not significantly different between valid, invalid, or neutral conditions [t's < 0.915, p's > 0.369].

The results of a cluster analysis found significantly less beta desynchronization between the required item hits and correct rejections between 0.8 and 1.25 seconds in a cluster of 16 right posterior electrodes [t(24)=4.175, p=0.001]. Follow-up analyses with this spatiotemporal cluster found significantly less desynchronization for valid [t(24)=2.836,p=0.009], invalid [t(24)=2.467, p=0.029], and neutral [t(24)=2.348, p=0.042] item hits compared to correct rejections. This old-new effect was significantly larger for the required compared to the valid [t(24)=2.645, p=0.013] condition, but was not reliably different from the invalid [t(24)=1.852, p=0.086], or neutral [t(24)=1.716, p=0.117] conditions.

Thus, there was significantly greater alpha desynchronization for valid, invalid, and neutral hits compared to correct rejections, and no difference in alpha desynchronization between the required condition and correct rejections. For beta there was significantly less desynchronization for all old item conditions compared to correct rejections, and the require condition had the least amount of desynchronization.

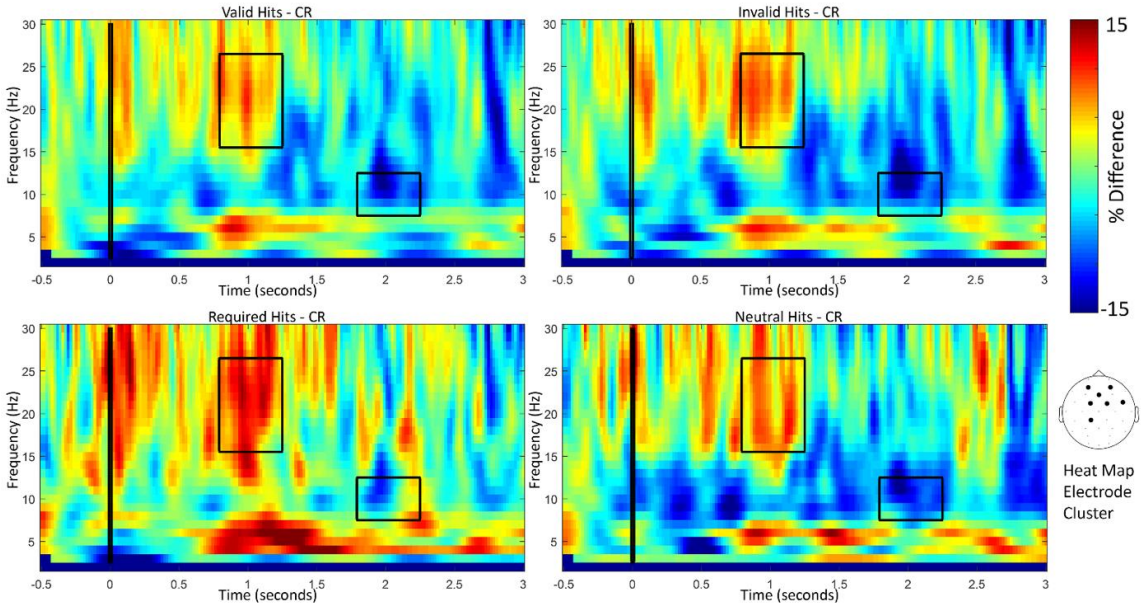

Figure 16: Heat maps are an average of the intersecting electrodes found in the alpha and beta frequency range.

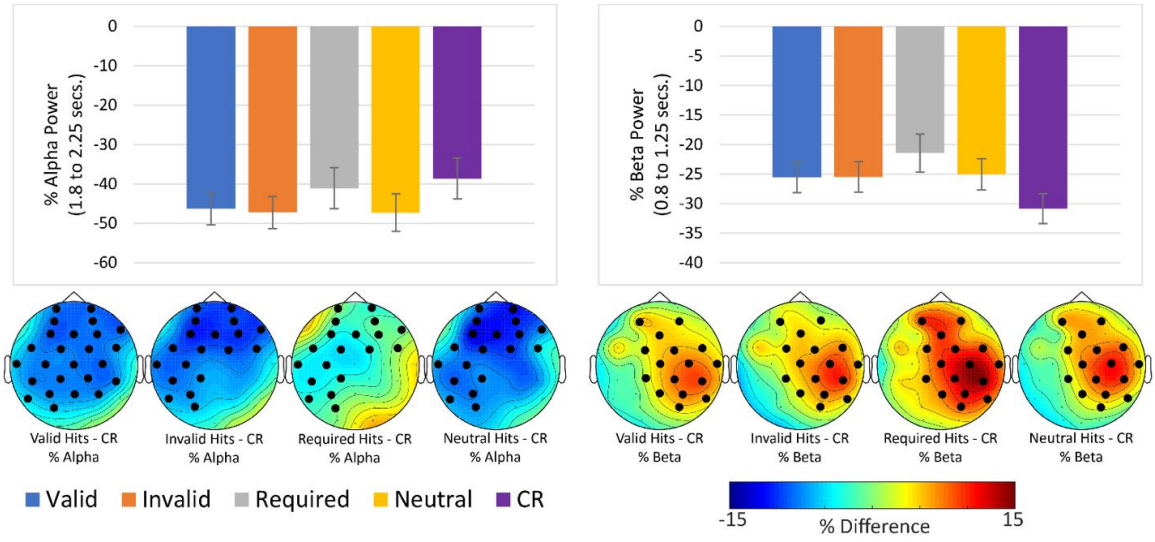

Figure 17: Error bars = 1 SEM. Bar charts represent average cluster power in each of our five conditions. Topographic maps are all four encoding conditions minus correct rejections.

APPENDIX B.

B.1 High Confidence Context Correct EEG Results

Confidence data was collected during retrieval. The following analyses are based on a high confidence ('sure' response) for context memory hits. Context memory misses included all confidence levels in order to maintain enough trials to analyze. As with the original analyses, only the valid and invalid conditions had enough power (trials) to investigate context memory performance. Two participants did not have enough high confident context hits in the invalid condition and were removed from the subsequent analyses. First, I reran the identified spatiotemporal clusters from the main context memory analyses, and then report the results from the spatiotemporal cluster that differ from those already reported in the main context analyses.

B.1.1 Replication of across confidence clusters

The cue – stimulus interval clusters during encoding from the across confidence analyses. For valid trials, I did not replicate the correlation between alpha power in the valid context memory contrast and the proportion of valid context memory hits across a cluster of 16 left posterior electrodes (1.8 to 2.7 seconds post-cue) [$r(21)=-0.211$, $p=0.335$]. This remained insignificant for the invalid trials [$r(21)=0.192$, $p=0.38$].
The post-stimulus interval clusters during encoding from the across confidence analyses. For invalid trials, significantly greater beta desynchronization was found for high confident context memory hits compared to context memory misses in the cluster of 20 central and posterior electrodes between 3.75 and 4 seconds post-cue (1.25 to 1.5 seconds

post-stimulus) [t(22)=-3.075, p=0.007]. This remained insignificant for the valid trials [t(22)=-1.215, p=0.245], although the invalid high confidence context memory contrast was not significantly greater compared to the valid high confidence context memory contrast [t(22)=1.763, p=0.119].

Context memory retrieval clusters from the across confidence analyses. Across both valid and invalid context memory trials the posterior cluster of 22 electrodes between 0.75 and 1.15 seconds post-stimulus in the alpha frequency band was greater for high confidence context memory hits compared to context memory misses [t(22)=-4.514, p=0.001]. This cluster remained significant within the valid condition [t(22)=-3.806, p=0.001], but not the invalid condition [t(22)=-1.182, p=0.298], although the valid effect was not significantly larger than the invalid effect [t(22)=-0.909, p=0.379]. In the beta band, the cluster across both conditions in 17 frontal central electrodes between 0.65 and 1.3 seconds post-stimulus remained significant [t(22)=-2.697, p=0.018], and remained significant for the invalid condition [t(22)=-2.303, p=0.032], but not the valid condition [t(22)=-1.697, p=0.113]. In addition, the invalid power difference was larger than the valid power difference [t(22)=-2.303, p=0.032]. For valid trials, the beta band cluster of 22 central electrodes between 2.6 and 3 seconds post-stimulus remained significant different between high confidence context hits and context misses [t(22)=5.147, p=0.001]. This effect was not found for invalid trials [t(22)=1.278, p=0.203], and the power differences were significantly different between the two context memory contrasts [t(22)=2.377, p=0.027]. For the high confidence invalid context memory contrast, the correlation between theta power and the proportion of high confidence context memory hits was not significant in the cluster of 22 electrodes between 0 and 0.5 seconds post-

stimulus [r(21)=0.199, p=0.362], nor the cluster of 20 electrodes between 0.9 and 2 seconds [r(21)=0.168, p=0.445]. These early and late, clusters remained insignificant for the valid condition [r(21)=-0.203, p=0.353] and [r(21)=-0.103, p=0.64], respectively. Interestingly, alpha power for high confidence context memory contrast switched between the invalid and valid condition. Across the alpha cluster of 17 electrodes, the proportion of high confidence valid context memory hits was positively correlated with the high confidence memory contrast [r(21)=0.448, p=0.032], while the relationship between alpha power and invalid trials was no longer significant [r(21)=-0.055, p=0.805], and the correlation coefficients were marginal different from each other [Fisher's p=0. 089].

B.1.2 Summary

During the cue – stimulus interval of the encoding task the correlation between alpha power and valid context memory was not replicated. For the encoding post-stimulus beta effect, I found the same pattern as the across confidence analysis, although the power differences between the valid and invalid conditions were slightly attenuated. During retrieval, I did not find a significant relationship between invalid theta power and high confidence context memory. I was able to find the same relationship of greater alpha desynchronization for high confident context memory hit vs context memory misses collapsed across valid and invalid trials. I also found greater beta desynchronization for high confident context memory hit vs context memory misses collapsed across valid and invalid trials, although it was attenuated in the valid condition. Interestingly, I found the correlation between alpha power within the high confidence context memory contrast and the proportion of high confidence context memory hits was no longer related to invalid

trials [r(21)=-0.055, p=0.805], but was positively correlated within the valid conditions [r(21)=0.448, p=0.032].

B.2 Spatiotemporal clustering

During encoding, spatiotemporal clustering found one cluster across 19 frontocentral electrodes (AF3, F7, F3, FC1, FC5, C3, CP1, Pz, CP2, C4, T8, FC6, FC2, F4, F8, AF4, Fp2, Fz, Cz) between 3.3 and 3.7 seconds post-cue (0.8 to 1.2 seconds post-stimulus) with greater alpha desynchronization for high confident context memory hits compared to context memory misses across both valid and invalid conditions [t(22)=-3.566, p=0.001]. This remained significant within the valid [t(22)=-3.656, p=0.002] and invalid [t(22)=-2.591, p=0.020] conditions, and the power differences between the valid and invalid contrasts were not significantly different from each other [t(22)=-0.139, p=0.904].

During retrieval, spatiotemporal clustering found alpha power differences between 0.75 and 1.2 seconds post stimulus as well as beta power differences between 2.6 and 3 seconds post-stimulus. Given the temporal overlap of these clusters with the previously identified clusters, they were not investigated further.

APPENDIX C.

Table 8: Survey Responses

Survey 1 Questions (After Encoding)	"Not at All"				"Very Much"	Mean	SD
How helpful were the label cues?	1	2	3	4	5	3.64	0.952
How often did you use the label cues to prepare?	1	2	3	4	5	3.8	0.764
How helpful was the neutral ('-----') cue?	1	2	3	4	5	3.12	1.641
How often did you use the neutral cues to prepare?	1	2	3	4	5	2.96	1.594
How engaging was the task?	1	2	3	4	5	2.92	1.382
How often did you find yourself mind wandering?	1	2	3	4	5	3.44	1.044
How difficult was the task?	1	2	3	4	5	2.36	1.114
Did you use the cues?	Yes (1)		No(0)			0.96	0.2
Did you use the cues to create a mental image of the upcoming scene?	Yes (1)		No(0)			0.72	0.542

Survey 2 Questions (After Retrieval)	"Not at All"				"Very Much"	Mean	SD
How engaging was the task?	1	2	3	4	5	3.72	1.061
How often did you find yourself mind wandering?	1	2	3	4	5	2.76	1.451
How difficult was the task?	1	2	3	4	5	2.72	1.137
What time did you wake up today?	Experiment Time - Wake up (In Hrs.)					2.98	1.924
How many hours of sleep did you get last night?	In Hrs.					7.68	1.802
What time was your last meal?	Experiment Time - Eating Time (In Hrs.)					2.56	4.475
Did you get hungry during the experiment?	Yes (1)		No(0)			0.36	0.49
What you like to be contacted about additional studies?	Yes (1)		No(0)			0.92	0.277

Note: Participants were instructed to eat something within a few hours of starting the study. All but three complied. Three participants ate the previous night.

APPENDIX D.

Table 9: Familiarization Cue to Encoding Cue Classification Accuracy

	Valid & Invalid	Valid	Invalid	Lures	Non-Lures
		All Frequency Bands			
All Electrodes					
All Trials	0.261 [0.038]	0.259 [0.040]	0.263 [0.054]	n.a.	n.a.
Context Hits	0.260 [0.041]	0.261 [0.048]	0.263 [0.075]	n.a.	n.a.
Context Misses	0.268 [0.060]	0.265 [0.069]	0.272 [0.090]	0.277 [0.120]	0.267 [0.100]
Frontal Cluster					
All Trials	0.255 [0.022]	0.259 [0.039]	0.248 [0.043]	n.a.	n.a.
Context Hits	0.257 [0.037]	0.266 [0.058]	0.240 [0.058]	n.a.	n.a.
Context Misses	0.255 [0.039]	0.249 [0.053]	0.263 [0.068]	0.271 [0.128]	0.263 [0.107]
Central Cluster					
All Trials	0.255 [0.035]	0.254 [0.045]	0.257 [0.047]	*n.a.*	*n.a.*
Context Hits	0.256 [0.042]	0.253 [0.053]	0.261 [0.062]	*n.a.*	*n.a.*
Context Misses	0.263 [0.054]	0.265 [0.062]	0.262 [0.093]	0.288 [0.133]	0.241 [0.118]
Posterior Cluster					
All Trials	0.268 [0.036]*	0.269 [0.047]+	0.264 [0.046]	n.a.	n.a.
Context Hits	0.265 [0.058]	0.269 [0.067]	0.265 [0.079]	n.a.	n.a.
Context Misses	0.278 [0.051]*	0.280 [0.078]+	0.282 [0.073]*	0.299 [0.141]+	0.275 [0.09]
Right Frontocentral Cluster					
All Trials	0.260 [0.028]+	0.266 [0.033]*	0.250 [0.059]	n.a.	n.a.
Context Hits	0.255 [0.039]	0.265 [0.052]	0.237 [0.079]	n.a.	n.a.
Context Misses	0.272 [0.051]*	0.275 [0.062]+	0.264 [0.086]	0.284 [0.175]	0.249 [0.091]
		Theta			
All Electrodes					
All Trials	0.256 [0.030]	0.265 [0.039]+	0.241 [0.044]	n.a.	n.a.
Context Hits	0.254 [0.042]	0.264 [0.056]	0.240 [0.063]	n.a.	n.a.
Context Misses	0.268 [0.043]*	0.274 [0.058]*	0.261 [0.069]	0.268 [0.120]	0.258 [0.065]
Frontal Cluster					
All Trials	0.253 [0.030]	0.254 [0.034]	0.251 [0.047]	n.a.	n.a.
Context Hits	0.248 [0.034]	0.237 [0.049]	0.270 [0.064]	n.a.	n.a.
Context Misses	0.271 [0.052]+	0.291 [0.062]**	0.244 [0.069]	0.25 [0.098]	0.235 [0.092]
Central Cluster					
All Trials	0.256 [0.033]	0.255 [0.038]	0.257 [0.045]	n.a.	n.a.
Context Hits	0.251 [0.044]	0.249 [0.052]	0.254 [0.076]	n.a.	n.a.
Context Misses	0.269 [0.041]*	0.270 [0.052]+	0.268 [0.068]	0.28 [0.135]	0.26 [0.087]
Posterior Cluster					
All Trials	0.266 [0.030]*	0.268 [0.039]*	0.262 [0.044]	n.a.	n.a.
Context Hits	0.269 [0.045]*	0.276 [0.068]+	0.264 [0.069]	n.a.	n.a.
Context Misses	0.268 [0.050]+	0.271 [0.081]	0.273 [0.078]	0.272 [0.141]	0.28 [0.101]
Right Frontocentral Cluster					
All Trials	0.259 [0.028]	0.253 [0.033]	0.268 [0.046]+	n.a.	n.a.
Context Hits	0.252 [0.038]	0.246 [0.056]	0.265 [0.060]	n.a.	n.a.
Context Misses	0.272 [0.047]*	0.270 [0.074]	0.277 [0.083]	0.247 [0.142]	0.299 [0.117]*
		Alpha			
All Electrodes					
All Trials	0.254 [0.037]	0.249 [0.047]	0.263 [0.046]	n.a.	n.a.
Context Hits	0.267 [0.051]	0.261 [0.062]	0.281 [0.072]*	n.a.	n.a.
Context Misses	0.241 [0.047]	0.229 [0.062]	0.262 [0.069]	0.263 [0.117]	0.266 [0.111]
Frontal Cluster					
All Trials	0.249 [0.034]	0.245 [0.035]	0.257 [0.053]	n.a.	n.a.
Context Hits	0.252 [0.032]	0.245 [0.041]	0.278 [0.079]+	n.a.	n.a.
Context Misses	0.246 [0.053]	0.240 [0.058]	0.261 [0.094]	0.252 [0.147]	0.269 [0.121]
Central Cluster					
All Trials	0.246 [0.031]	0.235 [0.037]*	0.267 [0.047]+	n.a.	n.a.
Context Hits	0.257 [0.044]	0.246 [0.057]	0.282 [0.082]+	n.a.	n.a.
Context Misses	0.243 [0.046]	0.227 [0.053]*	0.268 [0.069]	0.276 [0.127]	0.256 [0.092]

Posterior Cluster					
All Trials	0.253 [0.018]	0.248 [0.030]	0.261 [0.044]	n.a.	n.a.
Context Hits	0.255 [0.038]	0.251 [0.065]	0.263 [0.062]	n.a.	n.a.
Context Misses	0.254 [0.050]	0.251 [0.057]	0.257 [0.075]	0.238 [0.104]	0.270 [0.114]
Right Frontocentral Cluster					
All Trials	0.251 [0.028]	0.249 [0.036]	0.254 [0.035]	n.a.	n.a.
Context Hits	0.250 [0.043]	0.249 [0.050]	0.248 [0.067]	n.a.	n.a.
Context Misses	0.261 [0.045]	0.258 [0.063]	0.267 [0.080]	0.266 [0.132]	0.267 [0.114]
		Beta			
All Electrodes					
All Trials	0.252 [0.025]	0.256 [0.033]	0.248 [0.039]	n.a.	n.a.
Context Hits	0.247 [0.029]	0.250 [0.044]	0.242 [0.044]	n.a.	n.a.
Context Misses	0.259 [0.043]	0.266 [0.052]	0.251 [0.082]	0.233 [0.135]	0.263 [0.095]
Frontal Cluster					
All Trials	0.257 [0.030]	0.266 [0.042]+	0.241 [0.043]	n.a.	n.a.
Context Hits	0.258 [0.031]	0.270 [0.048]+	0.234 [0.055]	n.a.	n.a.
Context Misses	0.251 [0.048]	0.259 [0.076]	0.244 [0.073]	0.235 [0.131]	0.258 [0.105]
Central Cluster					
All Trials	0.244 [0.024]	0.242 [0.027]	0.247 [0.047]	n.a.	n.a.
Context Hits	0.242 [0.040]	0.247 [0.051]	0.234 [0.057]	n.a.	n.a.
Context Misses	0.250 [0.053]	0.241 [0.053]	0.263 [0.099]	0.264 [0.120]	0.260 [0.126]
Posterior Cluster					
All Trials	0.260 [0.024]+	0.265 [0.038]+	0.251 [0.048]	n.a.	n.a.
Context Hits	0.255 [0.042]	0.267 [0.071]	0.238 [0.085]	n.a.	n.a.
Context Misses	0.269 [0.037]*	0.269 [0.064]	0.275 [0.044]**	0.300 [0.119]*	0.266 [0.104]
Right Frontocentral Cluster					
All Trials	0.251 [0.031]	0.251 [0.041]	0.249 [0.046]	n.a.	n.a.
Context Hits	0.238 [0.044]	0.236 [0.062]	0.243 [0.076]	n.a.	n.a.
Context Misses	0.268 [0.059]	0.274 [0.077]	0.252 [0.090]	0.279 [0.150]	0.232 [0.107]

Note: Mean [SD]. + = p < 0.1, * = p < 0.05, ** = p < 0.01, *** = p < 0.001; Feature sets include 1 seconds of data from cue onset (10 0.1 second intervals)

Table 10: Familiarization Stimulus to Encoding Stimulus Classification Accuracy

	Valid & Invalid	Valid	Invalid	Lures	Non-Lures
		All Frequency Bands			
All Electrodes					
All Trials	0.255 [0.025]	0.262 [0.028]*	0.244 [0.044]	*n.a.*	*n.a.*
Context Hits	0.263 [0.040]	0.269 [0.049]+	0.257 [0.059]	*n.a.*	*n.a.*
Context Misses	0.237 [0.041]	0.251 [0.055]	0.213 [0.084]*	0.232 [0.115]	0.205 [0.110]+
Frontocentral Cluster					
All Trials	0.250 [0.029]	0.253 [0.034]	0.244 [0.049]	*n.a.*	*n.a.*
Context Hits	0.256 [0.044]	0.252 [0.048]	0.268 [0.059]	*n.a.*	*n.a.*
Context Misses	0.236 [0.048]	0.248 [0.063]	0.213 [0.093]+	0.206 [0.115]+	0.219 [0.115]
Parietal Cluster					
All Trials	0.256 [0.028]	0.259 [0.032]	0.251 [0.047]	*n.a.*	*n.a.*
Context Hits	0.244 [0.038]	0.244 [0.049]	0.252 [0.064]	*n.a.*	*n.a.*
Context Misses	0.271 [0.055]+	0.280 [0.077]+	0.263 [0.089]	0.276 [0.163]	0.266 [0.131]
Occipital Cluster					
All Trials	0.266 [0.030]*	0.272 [0.043]*	0.256 [0.033]	*n.a.*	*n.a.*
Context Hits	0.248 [0.044]	0.250 [0.063]	0.252 [0.046]	*n.a.*	*n.a.*
Context Misses	0.293 [0.046]***	0.307 [0.060]***	0.277 [0.071]+	0.318 [0.130]*	0.255 [0.102]
		Theta			
All Electrodes					
All Trials	0.253 [0.028]	0.259 [0.036]	0.243 [0.043]	*n.a.*	*n.a.*
Context Hits	0.252 [0.038]	0.255 [0.040]	0.248 [0.065]	*n.a.*	*n.a.*
Context Misses	0.250 [0.040]	0.261 [0.061]	0.235 [0.075]	0.207 [0.108]+	0.245 [0.100]
Frontocentral Cluster					
All Trials	0.254 [0.029]	0.255 [0.038]	0.253 [0.048]	*n.a.*	*n.a.*
Context Hits	0.258 [0.043]	0.254 [0.050]	0.269 [0.076]	*n.a.*	*n.a.*
Context Misses	0.248 [0.041]	0.258 [0.055]	0.235 [0.083]	0.215 [0.131]	0.241 [0.109]

Parietal Cluster					
All Trials	0.252 [0.023]	0.253 [0.031]	0.25 [0.036]	*n.a.*	*n.a.*
Context Hits	0.23 [0.049]+	0.229 [0.054]+	0.233 [0.07]	*n.a.*	*n.a.*
Context Misses	0.268 [0.044]+	0.274 [0.057]*	0.262 [0.069]	0.304 [0.155]+	0.233 [0.087]
Occipital Cluster					
All Trials	0.262 [0.027]*	0.263 [0.036]+	0.261 [0.025]*	*n.a.*	*n.a.*
Context Hits	0.251 [0.047]	0.253 [0.059]	0.250 [0.072]	*n.a.*	*n.a.*
Context Misses	0.272 [0.054]+	0.274 [0.069]+	0.276 [0.074]+	0.314 [0.141]*	0.25 [0.088]
		Alpha			
All Electrodes					
All Trials	0.257 [0.018]+	0.260 [0.028]+	0.252 [0.046]	*n.a.*	*n.a.*
Context Hits	0.245 [0.049]	0.245 [0.058]	0.248 [0.079]	*n.a.*	*n.a.*
Context Misses	0.260 [0.045]	0.268 [0.058]	0.250 [0.08]	0.241 [0.115]	0.255 [0.086]
Frontocentral Cluster					
All Trials	0.253 [0.026]	0.256 [0.032]	0.247 [0.042]	*n.a.*	*n.a.*
Context Hits	0.248 [0.044]	0.255 [0.050]	0.240 [0.069]	*n.a.*	*n.a.*
Context Misses	0.250 [0.043]	0.247 [0.061]	0.253 [0.067]	0.241 [0.116]	0.263 [0.089]
Parietal Cluster					
All Trials	0.255 [0.031]	0.258 [0.034]	0.251 [0.048]	*n.a.*	*n.a.*
Context Hits	0.237 [0.052]	0.237 [0.062]	0.235 [0.084]	*n.a.*	*n.a.*
Context Misses	0.261 [0.066]	0.261 [0.080]	0.258 [0.072]	0.263 [0.092]	0.254 [0.12]
Occipital Cluster					
All Trials	0.249 [0.027]	0.246 [0.034]	0.253 [0.047]	*n.a.*	*n.a.*
Context Hits	0.226 [0.051]*	0.223 [0.050]*	0.233 [0.069]	*n.a.*	*n.a.*
Context Misses	0.268 [0.042]*	0.277 [0.067]+	0.251 [0.084]	0.278 [0.119]	0.235 [0.111]
		Beta			
All Electrodes					
All Trials	0.249 [0.031]	0.250 [0.034]	0.248 [0.048]	*n.a.*	*n.a.*
Context Hits	0.245 [0.042]	0.246 [0.045]	0.243 [0.066]	*n.a.*	*n.a.*
Context Misses	0.247 [0.049]	0.251 [0.068]	0.241 [0.051]	0.243 [0.091]	0.240 [0.100]
Frontocentral Cluster					
All Trials	0.248 [0.024]	0.245 [0.034]	0.252 [0.034]	*n.a.*	*n.a.*
Context Hits	0.252 [0.021]	0.246 [0.035]	0.265 [0.051]	*n.a.*	*n.a.*
Context Misses	0.241 [0.049]	0.244 [0.070]	0.236 [0.056]	0.231 [0.097]	0.237 [0.075]
Parietal Cluster					
All Trials	0.248 [0.023]	0.243 [0.026]	0.257 [0.037]	*n.a.*	*n.a.*
Context Hits	0.239 [0.034]	0.239 [0.049]	0.236 [0.059]	*n.a.*	*n.a.*
Context Misses	0.253 [0.038]	0.241 [0.054]	0.267 [0.054]	0.270 [0.096]	0.271 [0.097]
Occipital Cluster					
All Trials	0.247 [0.033]	0.241 [0.034]	0.255 [0.047]	*n.a.*	*n.a.*
Context Hits	0.236 [0.057]	0.230 [0.056]+	0.245 [0.075]	*n.a.*	*n.a.*
Context Misses	0.258 [0.044]	0.255 [0.048]	0.260 [0.066]	0.250 [0.093]	0.275 [0.105]

Note: Mean [SD]. + = p < 0.1, * = p < 0.05, ** = p < 0.01, *** = p < 0.001; Feature sets include 1 seconds of data from stimulus onset (10 0.1 second intervals)

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