Interactions Between Attention and Memory

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
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ABSTRACT

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Abstract

Attention can take on many forms – it can be directed externally toward sensory information or internally toward self-generated information. It can be selective or sustained, and it can be goal-directed or spontaneous. A lot of research on attention-memory interactions has focused on selective, externally-directed attention, but we are constantly shifting between internally- and externally-directed attention and we can be distracted by both external and internal sources. There are also many instances in which we must maintain attention for long periods of time. To gain a more comprehensive understanding of the mechanisms by which attention and memory interact, more research is needed on the mnemonic consequences of the less investigated types of attention, such as internally-directed and sustained attention. In Chapters 2 and 3, I describe two electroencephalography (EEG) studies that investigated the neural mechanisms by which visual mental images that were generated during an internally-directed attention task are encoded into and retrieved from memory. Just as attention can be directed externally or internally, distraction can occur in various ways. For example, while listening to a lecture, our attention may be diverted toward the movement of the person seated next to us (an external distractor). Alternatively, attention can shift internally, towards random thoughts (an internal distractor). Both types of attention lapses will negatively affect encoding of the lecture, but may do so in

different ways. In Chapter 4, I describe a simultaneous pupillometry-fMRI study that investigated the fluctuations of sustained attention with the presence of both external and internal distractors as well as the impact on subsequent memory. Finally, we must consider the role that cognitive control plays in modulating interactions between attention and memory. In Chapter 5, I describe a behavioral study that investigated the cognitive control processes triggered in response to an error and their impact on subsequent memory. Taken together, these 4 studies provide a more nuanced look at the mechanisms by which attention memory interact as we process information in different ways.

Dedication

To the most supportive team I could've asked for: Анѓел, Тања, и Драган

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1. Introduction

When sitting in a lecture, multiple dynamics are at play as we try to focus on the presentation for a prolonged period of time. For example, we may frequently shift between directing attention towards the speaker or to our internal thoughts to process the presented information and tie it to existing knowledge. At some points, we may be more attentive towards the speaker so as to not miss an important claim, and at other points, we may be more attentive to our internal thoughts while critically analyzing a claim that was made. At the same time, we can also be distracted by both external influences, such as whispering in the back of the room, or internal thoughts, such as reminiscing on a movie we watched the night before. This example illustrates two concepts: (1) how we can direct attention to the external environment or our internal thoughts, and (2) how we can focus our attention in an intentional and goal-directed way as well as how attention can be captured incidentally. All of these dynamics are important to consider as we try to understand how we process information and which of that information is ultimately remembered.

Chun et al., (2011) proposed a taxonomy distinguishing between external and internal attention to emphasize the targets of attention instead of its mechanisms. Specifically, they defined the selection and modulation of sensory information (including objects, features, and spatial locations) as external attention and internally-generated information (such as task rules or the contents of working memory and long-term memory) as internal attention. However, much of the research that has investigated interactions between attention and memory has focused on external attention (Aly & Turk-Browne, 2017; Chun & Turk-Browne, 2007). To better delineate the processes at play, more research is needed on the interactions between internally-directed attention and memory as well as the mechanisms by which we switch between internal and external attention in order to understand their unique interactions with episodic memory. In the paragraphs below, I will discuss prior research that has focused on interactions between external attention and memory as well as internal attention and memory. Following this overview, I will review findings related to the mechanisms underlying the coordination of external and internal attention and their mnemonic consequences.

1.1 External attention

External attention refers to attention that is directed towards the external environment and to the processing of incoming sensory information. Attention modulates processing within all five senses (vision, hearing, touch, smell, and taste), but for the purposes of this review, I will focus on visual attention. External attention can be incidental (including bottom-up features of attention) or goal-directed (including top-down features of attention). When incidental, external attention is stimulus-driven and can be captured reflexively by the sudden appearance of an unexpected stimulus, for example, which orients attention towards the item (Simons, 2000; Yantis & Hillstrom, 1994). Even stimuli that have not been consciously perceived, as demonstrated by priming studies, can be processed incidentally (Dehaene et al., 1998; Greenwald et al., 1996). The ventral attention network (VAN), which includes the temporoparietal junction, middle frontal gyrus, and inferior frontal gyrus, contributes to bottom-up attention by detecting and shifting attention to unexpected stimuli (Corbetta et al., 2008; Vossel et al., 2014). Conversely, when external attention is goal-directed, the dorsal attention network (DAN), which includes the intraparietal sulcus, superior parietal lobule, and the frontal eye fields, supports maintenance of attention to environmental features and links this information to motor responses (Corbetta & Shulman, 2002; Vossel et al., 2014). One example is a visual search task, in which participants would have to shift attention to different spatial locations to identify an item in an array. Coupling with the DAN, the frontoparietal control network (FPCN) supports intentional shifts between environmental features. The FPCN includes the dorsolateral prefrontal cortex, anterior intraparietal sulcus, the rostrolateral prefrontal cortex, the presupplementary motor area (anterior to the supplementary motor area), and the inferior temporal gyrus (Kompus et al., 2009; Ramnani & Owen, 2004; Vincent et al., 2008).

1.1.1 External attention and memory

Attending to stimuli in our external environment improves subsequent memory for those items (Dudukovic, Preston, Archie, Glover, & Wagner, 2011; Gazzaley, Cooney, McEvoy, et al., 2005; Yi & Chun, 2005). When attention is divided by having to perform a secondary task, studies have shown a negative impact on subsequent memory performance (Baddeley, Lewis, Eldridge, & Thomas, 1984; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Mickley Steinmetz et al., 2014; Naveh-Benjamin & Brubaker, 2019; Uncapher & Rugg, 2005). In particular, goal-directed external attention leads to enhanced processing of task-relevant information and reduced processing of task-irrelevant distractors (Miller & Cohen, 2001; Noudoost et al., 2010). Thus, these top-down processes prepare individuals to encode only the task-relevant information. Studies using a subsequent memory paradigm and electrophysiological recordings have found increased pre-stimulus alpha rhythm (which has been linked to goal-directed attention; Cooper et al., 2003; Klimesch et al., 2007) associated with enhanced memory for task-relevant items (Fell et al., 2011) and reduced memory for task-irrelevant items (Park et al., 2014). Functional MRI (fMRI) studies have shown that lateral prefrontal cortex (PFC) can direct attention toward goal-relevant stimuli (Desimone & Duncan, 1995; Miller & Cohen, 2001), and greater encoding activation in the lateral PFC has been observed for subsequently remembered stimuli (Kim, 2011; Spaniol et al., 2009). Furthermore, when the engagement of regions implicated in goal-directed attention is insufficient, memory for task-irrelevant information is enhanced (Minamoto et al., 2012). Moreover, top-down attention has been shown to be more effective in promoting successful encoding even during distraction. One study compared subsequent memory for two types of distractors – one that captured attention because it matched the target defining feature and one that captured attention because it was perceptually salient (Sasin & Fougnie, 2021). Results showed equivalent levels of attentional capture for both distractors but improved memory for the distractors with target-matching features. However, when attention is captured by an irrelevant distractor, memory for the task-relevant information is impaired (Uncapher & Wagner, 2009). Greater activity in the temporoparietal junction, which has been implicated in reorienting, has been linked to reduced memory for task-relevant items (Turk-Browne et al., 2013). Taken together, these findings suggest that engagement of cognitive control processes may be particularly predictive of subsequent memory.

1.2 Internal attention

In contrast to external attention, internal attention refers to attention directed towards thoughts and information that has been previously stored in order to process this internally generated information (Chun et al., 2011; Dixon et al., 2014). This can include memory retrieval, mental simulation, stimulus-independent thoughts, or mental imagery (Andrews-Hanna, 2012; Buckner et al., 2008; Buckner & DiNicola, 2019). An external stimulus may be present for internal attention, however, the processing in internal attention is generally decoupled from the external environment (Dixon et al., 2014; Schooler et al., 2011). Previous electrophysiology studies have demonstrated that both early sensory-level processing (as reflected by the visual P1 and auditory N1 event-related potential components [ERPs]) and late higher order processing (as captured by the P3) are reduced during periods of internal attention that is stimulus-independent (Fell et al., 2011). Critically, this reduced response is observed for distractors as well, which suggests that the reduction of external attention arises from an internal focus that is necessary to maintain the stimulus-independent thought.

Just like external attention, internal attention can be either incidental or goal-directed. Incidental internal attention refers to cognitive states in which attention is involuntary (commonly referred to as mind-wandering; Schooler et al., 2011). Goal-directed internal attention occurs when attention is voluntarily directed internally, such as when planning out the day or during visual mental imagery and mental simulation. The key brain areas associated with internal attention are part of the default mode network (DMN; Buckner et al., 2008; Buckner & DiNicola, 2019), which consists of three functionally distinct subsystems. The core subsystem, made up of the anterior medial prefrontal cortex, posterior cingulate cortex, and posterior inferior parietal lobule, serves as a hub (Andrews-Hanna et al., 2010). The second subsystem centers around the medial temporal lobe, including the hippocampal formation and parahippocampal cortex, and plays a role in memory and mental simulation (Andrews-Hanna et al., 2014; Buckner et al., 2008; Buckner & Carroll, 2007; Schacter et al., 2007). The third subsystem includes the dorsomedial prefrontal cortex and lateral temporal cortex and has been linked to mentalizing as well as conceptual and emotional processing (Andrews-Hanna et al., 2014). Experience sampling studies using fMRI have shown increased activity in the DMN during periods of internal attention (Christoff et al., 2009; Stawarczyk, Majerus, Maquet, et al., 2011). On the other hand, studies have shown that during an externally-directed attention task, a decrease in activity in posterior midline regions, including the precuneus and posterior cingulate, correlates with improved subsequent memory (Daselaar et al., 2004; de Chastelaine & Rugg, 2014).

While the first and third neural subsystems are more active during internal attention, the subsystem centering around the medial temporal lobe does not display differential activation to internal compared to external attention (Christoff et al., 2009; Stawarczyk, Majerus, Maquet, et al., 2011). Instead, this subsystem is recruited when subjects are unaware that they are mind-wandering compared to when they are aware, which suggests its role is more specific to incidental internal attention, since attention presumably cannot be goal-directed when there is an absence of awareness (Christoff et al., 2009). In an fMRI study designed to detect the onset of incidental thoughts in trained mindfulness (a goal-directed internal attention task) practitioners showed recruitment of the medial temporal lobe subsystem of the DMN immediately before incidental thoughts arose (Ellamil et al., 2016). To support goal-directed internal attention, the FPCN can flexibly couple with the DMN, just as it couples with the DAN to support goal-directed external attention (Spreng et al., 2010). Within the FPCN, the lateral PFC is consistently activated during goal-directed internal attention (Banich, 2009; Christoff &

Gabrieli, 2000; Duncan & Owen, 2000; Prado et al., 2011), such as when making future plans (Spreng et al., 2010) and during episodic memory retrieval (Barredo et al., 2015). Research has shown that when internal attention shifts to spontaneous (incidental) thoughts during mindfulness, the FPCN becomes active as subjects disengage from the spontaneous thoughts and redirect attention towards the goal-directed task.

1.2.1 Internal attention and memory

To date, the research investigating interactions between internal attention and memory has been limited. Studies on mental imagery (an goal-directed internal attention task) have reported that use of imagery during encoding improves memory performance (Bower, 1972; D'Angiulli et al., 2013a; Foley, 2012; Gupton & Frincke, 1970; Katz, 1981; McCauley et al., 1996; Mueller & Jablonski, 1970; Richardson, 1977; Verhaeghen et al., 1993). Yi et al., (2008) also investigated the influence of goal-directed internal attention (specifically memory retrieval) on memory. Here, subjects were presented with a series of scenes. Over two frames, the scene was presented once in the first frame and either presented for a second time in the second frame, or subjects were instructed to refresh the scene in their mind's eye in order to make a category judgment. In comparison to scenes that were only presented once, memory was similarly improved for both the scenes that were presented twice and those that were mentally refreshed the second time, indicating that goal-directed internal attention (seeing the image in your ‘mind’s eye’) can improve memory as well as external attention (seeing the image visually).

Mind-wandering has frequently been shown to impair encoding, leading to worse subsequent memory (Garlitch & Wahlheim, 2020; Maillet & Rajah, 2013; Peterson & Wiseman, 2020; Seibert & Ellis, 1991; Smallwood et al.., 2004; Smallwood et al., 2003a; Smallwood et al., 2003b; Xu & Metcalfe, 2016; Blonde et al., 2021; Chinchannachokehai et al., 2020a; deBettencourt et al., 2018; Krasich et al., 2018; Zhang et al., 2021). One study manipulating depth of encoding (Thomson et al., 2014), used thought probes to assess instances of mind-wandering while participants viewed a series of words and made either size judgements comparing the item to a computer monitor (semantic encoding) or case judgements (perceptual encoding). Results showed impaired memory during instances of mind-wandering only for the semantic encoding condition and not the perceptual encoding condition, while rates of mind-wandering were similar across conditions. Another study reported that during shallow encoding, improved memory was observed during mind-wandering when the thoughts were stimulus-dependent (Maillet & Schacter, 2016b). This suggests that when cognitive resources are taxed, the mnemonic consequences of internal attention increase. Thus, across both external and internal attention, engagement of cognitive control processes leads to improved memory performance, while incidental attention leads to worse memory. To further explore these mnemonic consequences, we must investigate the interactions between external and internal attention.

1.3 Coordination of external and internal attention

While it is important to study external and internal attention in isolation, throughout the day we are continuously shifting between the two. Due to research showing that periods of internal attention are associated with poor task performance on an external, goal-directed task (Allen et al., 2013; Kam & Handy, 2014; Smallwood, McSpadden, et al., 2008; Smallwood & Schooler, 2006) and that activity in the DMN, which is associated with internal attention, is negatively correlated with activity in the DAN (Fox et al., 2005), external and internal attention have appeared to be mutually exclusive. However, Dixon et al., (2014) have suggested that external and internal attention are not inherently antagonistic and can co-occur with some limited interference on task performance if one or both processes are incidental. When external and internal attention are incidental, they are driven by distinct lower-order regions that can operate concurrently. If, instead, both external and internal attention involve higher levels of cognitive control using directed, top-down processing, there is competition for the capacity-limited resources where the processing streams converge. Thus, competition between external and internal attention occurs when recruiting overlapping higher-order regions.

Previous MRI studies suggest how this might occur. As previously mentioned, past studies have shown that the FPCN, and in particular the lateral prefrontal cortex (PFC), play a role in both external and internal attention (Corbetta & Shulman, 2002; Miller & Cohen, 2001; Spreng et al., 2010). Spreng and colleagues (2010) observed functional coupling both between the FPCN and DMN during an autobiographical planning task and between the FPCN and DAN during a visuospatial planning task. Moreover, the lateral PFC is anatomically situated between the DMN and DAN, allowing it to integrate information about competing stimuli from both networks (Vincent et al., 2008). In addition, human lesion studies have confirmed a causal role of the lateral PFC in external attention with observed deficits in a visual detection task (Barceló et al., 2000). Similarly, Kam et al., (2018) demonstrated dysregulation in patients with damage to the lateral PFC for both external and internal attention, with results showing increased frontocentral midline theta power during external attention and increased alpha power during internal attention in healthy controls, but no observed differences in patients with lateral PFC lesions. With the FPCN playing a role in both external and internal attention, it is important to investigate its role in the interaction between external and internal attention.

In a connectivity-based parcellation of the brain by Yeo et al., (2011), two fronto-parietal subsystems of the FPCN were reported and recently supported by a study examining patterns of FPCN functional connectivity to test for heterogeneity within the

FPCN (Dixon et al., 2018). Using hierarchical clustering and classification analysis, researchers identified two subsystems of the FPCN (FPCN$_{\text{A}}$ and FPCN$_{\text{B}}$), which were differentially coupled with the DMN and DAN. The two subsystems were separated based on intramodular connections as well as intermodular connections with the DMN and DAN, and they were spatially distinct. FPCN$_{\text{A}}$ nodes included the middle temporal gyrus, rostrolateral prefrontal cortex, middle frontal gyrus, superior frontal gyrus, anterior inferior parietal lobule, and presupplementary motor area. The FPCN$_{\text{B}}$ nodes included the posterior middle temporal gyrus, inferior frontal sulcus, posterior superior frontal gyrus, and the intraparietal sulcus.

FPCN$_{\text{A}}$ was coupled with the DMN and functional domains that activate the DMN, including topics related to mentalizing. This suggests a role for FBCN$_{\text{A}}$ in enabling free modes of thought unconstrained by sensorimotor interactions. In contrast, FPCN$_{\text{B}}$ was functionally connected to the DAN and topics related to attention and action, suggesting a role of top-down control over the DAN to keep attention on the relevant task. Specifically, FPCN$_{\text{B}}$ encodes task-relevant information on the basis of goals and expected outcomes (Bunge et al., 2003; Dixon & Christoff, 2012; Stokes et al., 2013). These coupling patterns were observed within each individual subject, as well as across three datasets, suggesting that these two subsystems, at least in part, modulate external and internal attention distinctly through functional connections with the DAN and DMN, respectively.

A recent study by Kam et al., (2019) investigated the electrophysiological mechanisms underlying the communication between the FPCN and DMN using intracranial EEG and provided support for these functional connections. Participants performed an external attention task, during which frequent non-target tones and infrequent target tones were presented, and they were instructed to respond when they heard a target. On the other hand, in the internal attention condition, they were instructed to ignore the tones and focus on any thoughts that came to mind. With this paradigm, the stimulus set remained identical across both conditions so that any electrophysiological differences between conditions could be attributed to the differing attention states. Results showed enhanced theta connectivity between the DMN and FPCN$_A$ during internal attention as opposed to external attention, and the level of connectivity was predictive of subjects' ratings of the amount of time they spent directing attention internally. In addition, connectivity between the DMN and FPCN$_B$ did not differ between attention states. Previous studies have reported enhanced theta connectivity both within the DMN during internal attention (Foster et al., 2016) as well as within the FPCN during intentional attention (Fellrath et al., 2016). Thus, this study suggests that the theta connectivity between these two networks could reflect an integration of these processes to support goal-directed internal attention.

The third FPCN subsystem consisting of parietal regions only was supported by a meta-analysis by Kim, (2018). This study suggested that the parietal control network

(PCN), referring to the parietal components of the FPCN, plays a role in facilitating the co-occurance of external and internal attention. Specifically, the PCN consists of the precuneus, mid-cingulate cortex, and lateral intraparietal sulcus. Past research has implicated the precuneus as the local hub linked to the rest of the FPCN through the lateral intraparietal sulcus (Rosen et al., 2016). One study analyzed brain activity of 10 different cognitive tasks and showed activity in the precuneus, mid-cingulate cortex, lateral intraparietal sulcus, and other FPCN regions over a majority of the tasks, suggesting that these regions play a role in facilitating goal-driven tasks (Dosenbach et al., 2006). However, additional task-based studies are needed to further investigate these subsystems. Taken together, these studies demonstrate the neural mechanisms by which external and internal attention may co-occur, thereby providing support for the framework proposed by Dixon et al., 2014, which asserts that external and internal attention are not inherently antagonistic. However, it is important to further investigate the level of interference that occurs when these processes co-occur and whether it varies based on the direction of the intentional attention. Investigating these interactions under different levels of cognitive control engagement can offer insight into the mechanisms that facilitate or inhibit memory, which may vary in the presence of external compared to internal distractors.

When attention is external and goal-directed, interference can be caused by external distractors capturing attention incidentally, internal thoughts capturing attention incidentally, or a goal-directed shift towards internal attention. Similarly, when attention is goal-directed and internal, interference can be caused by external distractors capturing attention incidentally, internal thoughts capturing attention incidentally, or a goal-directed shift towards external attention. Direct comparisons are needed to investigate the levels of interference that occur within goal-directed external and internal attention, based on the different ways in which attention can shift away from the task at hand. In addition, comparisons are needed to investigate differences between goal-directed external and internal attention in their susceptibility to interference.

In a study that cued participants to switch between external and internal attention on a trial-by-trial basis (Verschooren, Pourtois, & Egner, 2020), results showed a larger switch cost when switching toward internal attention, suggesting that shielding internal attention from external intrusions is more efficient. Similarly, a study by Ziegler et al., (2018) examined the impact of both internal and external distractors in internally and externally oriented tasks to determine the role attentional state plays on distraction regulation. Results showed that an external distractor (auditory sound) decreased performance in the externally oriented task while also leading to suppression of internal distractors. Furthermore, performance on the externally oriented task was predicted by the degree of suppression of the internal distractors. Conversely, the external distractor did not have an impact on performance in the internally oriented task. Thus, goal-directed internal attention is somehow protected from the external distractor. Additional research is also needed to investigate how interference is modulated by time-on-task as cognitive control resources decrease and motivation to direct attention elsewhere increases, such as during sustained attention.

1.4 Mnemonic outcomes of interactions between external and internal attention

In addition to examining the causes of these fluctuations between internal and external attention, it is critical to investigate how they affect ongoing information processing. In a typical sustained attention task, for example, attention is mostly goal-directed and external (task-focused). However, over the course of the task, we lose focus, either because attention is captured by something distracting in the environment or by an internal thought. In addition, over time, due to either boredom or decreased motivation to complete the task at hand, attention may shift to internal thoughts. In all three cases, we would expect a lapse in attention to occur, but the differences in the neural mechanisms that underly each type of lapse are not well understood.

The closest investigation to this question is a study in which subjects were instructed to learn word-pairs while completing a secondary task that was either external (tone discrimination) or internal (monitor their own thoughts; Bonhage et al., 2016). Behaviorally, dividing attention with either the external or internal secondary (goal-directed) task led to similar impairments in memory performance. However, the internal secondary task was associated with increased activation of the medial prefrontal cortex (a key node of the default mode network; Andrews-Hanna, 2012; Sridharan et al., 2008), as well as the anterior cingulate cortex and anterior insula, which are regions that have been linked to performance monitoring (Menon & Uddin, 2010a; Sridharan et al., 2008). In contrast, the secondary external task was associated with reduced activity in the hippocampus, a core memory region. These results suggest that both distractor tasks impaired learning but for different reasons: the external secondary task disrupted basic memory processes (hippocampus) whereas the internal secondary task shifted attention towards internal monitoring (medial prefrontal cortex, anterior cingulate cortex and anterior insula). In this case, attention was divided between two tasks that were both goal-directed. According to Dixon et al.'s (2014) framework, this leads to competition between internal and external attention as their processing streams converge, which could explain the shift towards internal monitoring. Since lapses in sustained attention can also be caused by both external and internal distractors, the neural mechanisms that shape the interactions between sustained attention and subsequent memory may also be distinct and differentially influenced by changes in cognitive control and motivation. Additional research is needed to directly compare the different types of lapses in attention.

Some research has suggested a positive outcome for shifts toward internal attention. While incidental internal attention may have negative mnemonic consequences for items encountered while attention is shifted internally, the overall mnemonic consequence of periodically shifting attention internally could be positive.

During an external, goal-directed task, a shift to internal attention may play a role in dishabituation (Schooler et al., 2011). In this case, stimulus-independent thoughts provide a necessary break from the task so the subjects can return with refreshed capacity. In fact, studies have shown that memory performance increases when information is spaced out over time (Cepeda et al., 2006; Metcalfe & Xu, 2016). Researchers have also suggested a role for incidental internal attention in memory consolidation given its neural dynamics (Meyer et al., 1990; Mildner & Tamir, 2019; Wamsley, 2019). The default variability hypothesis (Mills et al., 2018) suggests that the variability of spontaneous thought content facilitates encoding of separate episodic events by supporting pattern separation through randomized memory reactivation that de-correlates memory representations from one another. Separating the memory traces in this way can strengthen the representations of the underlying features and thereby improve memory efficiency. Furthermore, the repeated reactivation supports the integration of memories into semantic knowledge by promoting the generalization of information from episodic memory. Further research is needed to directly test this hypothesis and disentangle how it might be modified when distinguishing between shifts towards internal attention that are due to failures in cognitive control vs decreased motivation.

1.5 Conclusion

The research reviewed in this chapter has shown that attention is critical to successful memory encoding. However, we know that attention be external or internal, it can be goal-directed or incidental, and it can be selective or sustained. To gain a better understanding of some of the less investigated nuances of attention-memory interactions, I will describe four studies that focus in on some of these specific types of attention. In Chapters 2 and 3, I will describe two studies that investigate interactions between internal attention and memory. More specifically, these studies use electroencephalography (EEG) to investigate the mechanisms by which internally-generated information (specifically visual mental imagery) is encoded into and retrieved from episodic memory. Furthermore, these studies examine the impact of the quality of the internally-generated information (represented by the vividness of the visual mental imagery) on the encoding and retrieval processes. In these chapters, goal-directed internal attention is referred to more briefly as internally-directed attention. In Chapter 4, I will examine the impact of external and internal distractors on subsequent memory. In this study using pupillometry and MRI methods, I investigate interactions between sustained attention and memory with a comparison between external and internal distractors. Finally, to more broadly examine the role of cognitive control in modulating attention-memory interactions, in chapter 5, I will describe a behavioral study that investigates how errors lead to adjustments in cognition that influence attention and impact target and distractor encoding.

2. The influence of imagery vividness and internally-directed attention on the neural mechanisms underlying the encoding of visual mental images into episodic memory

2.1 Introduction

While sitting in a history class, your attention may be directed externally to the professor giving a lecture about a war, but you may also regularly shift your attention internally to form a mental image of a battle scene that is being discussed. Both externally- and internally-directed attention can determine your ability to learn, as both the external and internal attentional processes contribute to being able to successfully later remember the contents of the lecture. Chun et al., (2011) proposed a taxonomy distinguishing between externally- and internally-directed attention in terms of the target of the attentional focus. More specifically, they defined externally-directed attention as the selection and modulation of sensory information (including objects, features, and spatial locations), and internally-directed attention as attention directed toward internally-generated information (such as task rules, mental imagery, or the contents of working memory and long-term memory). Although this distinction is fundamental, the vast majority of cognitive neuroscience research on attention has focused on externally-directed attention (for review, see Aly & Turk-Browne, 2017; Chun & Turk-Browne, 2007), and very little is known regarding the neural mechanisms of internally-directed attention and its impact on other cognitive processes. The overarching goal of the current study was to investigate the neural mechanisms by which internally-directed attention contributes to episodic memory encoding.

We employed a form of the hallmark ‘subsequent memory paradigm’, which compares encoding activity for subsequently remembered versus subsequently forgotten items (Friedman & Johnson Jr., 2000; Paller & Wagner, 2002). In electroencephalographic (EEG) and event-related-potential (ERP) studies, the most investigated subsequent memory effect has been the *difference due to memory* (Dm), a broadly distributed, centro-parietal ERP during encoding occurring at ~400-800 ms after stimulus onset (Johnson, 1995; Paller et al., 1987, 1988; Wagner et al., 1999). Previous research has shown that the Dm can be modulated by directing attention towards the conceptual or semantic meaning of an item, with a greater Dm observed for deeper levels of encoding (Guo et al., 2004; Paller et al., 1987). This finding has led to the suggestion that the Dm increases with conceptual processing, which is well known to enhance memory encoding (Craik & Lockhart, 1972; Craik & Tulving, 1975).

To date, however, research investigating interactions between internally-directed attention and memory has been limited. One of the few exceptions is the study by (Yi et al., 2008). In this study, each trial consisted of two frames. In the first frame, participants viewed a scene, and in the second frame, they either viewed the scene again or generated a mental image of the scene. In comparison to viewing scenes only once, memory was improved, and to a similar degree, by viewing scenes twice and by viewing the scene once and then imagining it. These results suggest that internally-directed attention (seeing the image in your ‘mind’s eye’) improved memory as much as externally-directed attention could.

Relatedly, studies investigating the generation of mental images (a goal-directed attention task) have reported that the use of imagery during encoding improves memory performance (Bower, 1972; D’Angiulli et al., 2013b; Foley, 2012; Gupton & Frincke, 1970; McCauley et al., 1996; Mueller & Jablonski, 1970). The quality of the imagery can vary from item to item, with some mental images being highly detailed and vivid and others being very poor (Cui et al., 2007). Vividness has been defined as a construct that expresses the self-reported degree of richness, level of detail, and clarity of a mental image in comparison to actually seeing the imagined stimulus (D’Angiulli & Reeves, 2007). An fMRI study investigating vividness in mental imagery confirmed the link between imagined and perceived stimuli with results showing that the neural overlap between imagery and perception in the visual system correlated with experienced imagery vividness (Dijkstra, Bosch, & Gerven, 2017). Studies have also shown improved memory for mental images that had been visualized with high vividness (D’Angiulli et al., 2013b; De Beni & Pazzaglia, 1995), suggesting that the vividness influences subsequent memory. However, the neural mechanisms by which mental images of high versus low vividness are successfully encoded into episodic memory have been little studied.

To investigate the neural mechanisms that support the successful encoding of internally-generated information into episodic memory, we designed an incidental encoding task during which participants formed visual mental images, a task which requires internally-directed attention. While an external stimulus may be present during internally-directed attention, the processing seems to be generally decoupled from the external environment (Dixon et al., 2014; Schooler et al., 2011). Previous electrophysiology studies have demonstrated that both early sensory-level processing (as reflected, for example, by the visual P1 and auditory N1 ERP sensory components) and late higher-order processing (as captured by the hallmark P3 ERP wave) are reduced during periods of internally-directed attention (Baird et al., 2014; Smallwood, Beach, et al., 2008). However, shifts from externally- to internally- directed attention are difficult to measure, as they occur covertly. Our novel alternative to the difficult task of measuring the neural correlates of internally-directed attention was to use *steady-state visual evoked potentials* (SSVEPs), typically used as a measure of externally-directed attention, to index internally-directed attention instead. The SSVEP is an oscillatory EEG response that resonates at the same frequency as a flickering stimulus and is modulated by externally-directed attention to that stimulus, with an increase in SSVEP power at that frequency reflecting increased selective attention to that stimulus (Morgan et al., 1996; Muller et al., 2006; Vialatte et al., 2010). Accordingly, it stands to reason that a *decrease* in SSVEP power to an externally flickering stimulus, which reflects a shift of externally-directed attention away from that stimulus, could correspondingly, but inversely, reflect at least in part a shift towards internally-directed attention to form the mental image as instructed. Thus, SSVEPs could serve as a high-temporal-resolution index of the external versus internal orientation of attention. More specifically, in the present study we made such use of SSVEPs to index internally-directed attention during visual mental imagery in an incidental encoding task.

Participants were presented with a series of flickering object-word stimuli and tasked with forming a mental image of the object denoted by each of the words and rating the image vividness (**Fig 1**). They then completed a surprise memory retrieval task, in which they were presented with both old and new words, and instructed to identify which items were old or new, including rating their confidence of that assessment. Our hypotheses were focused on the attention-related processes during the visual mental imagery, indexed by the SSVEPs, and the high-level encoding-related processes, indexed by the Dm. We hypothesized that our behavioral results would show improved memory for the high-vividness items, but we in particular wanted to examine the neural mechanisms underlying the successful encoding of high-vividness versus low-vividness items into episodic memory.

The study had three main goals. The first was to investigate the use of SSVEPs to track shifts between externally- and internally-directed attention. We hypothesized that after reading the flickering word stimulus, the process of forming a mental image of the object denoted by the word would result in a decrease of the SSVEP driven by the externally presented flickering word stimulus, which would then return to baseline as the imagery process was completed and attention returned to the visual screen.

Our second goal was to investigate the relationship between SSVEPs and the quality of mental images. Given the paucity of evidence regarding mental images and SSVEPs, we entertained two hypotheses regarding vividness. One hypothesis was that if participants deployed greater internally-directed attention and/or spent more time forming the mental images, they would be able to form images of better quality. If so, compared to images rated as low-vividness, images rated as high-vividness would be associated with a larger and/or longer decrease in the SSVEP. The alternative hypothesis was that because a rating of low-vividness would indicate that the participant struggled with forming the image, the effect would be exactly the opposite, such that the low-vividness images would instead be associated with a larger and/or longer-duration SSVEP decrease. Given the prior research demonstrating faster RTs for more vivid mental images (D'Angiulli et al., 2013b), however, and assuming that the internally-directed attention indexed by the SSVEP would be in line with RTs, we predicted that the second hypothesis would be more likely.

Finally, our third goal was to examine the influence of image vividness on the conceptually-related Dm effect during the image-generation period. We hypothesized that the elicitation of an enhanced Dm effect for the subsequently remembered high-vividness items could reflect greater encoding due to increased perceptual saliency. Alternatively, if there was a larger or more sustained Dm effect for the remembered low-vividness items, a plausible interpretation could be that enhanced conceptual processing is needed to compensate for the poor mental image in order to still be remembered.

2.2 Methods

2.2.1 Participants

Thirty-one healthy participants between the ages of 18 and 35 years (*M* = 23.0, *SD* = 3.39) were recruited through the Duke University Psychology Subject Pool and Interdisciplinary Behavioral Research Center. All participants were right-handed with normal or corrected-to-normal vision and no history of neurological or psychiatric disease. Informed consent was obtained for all participants for their credited (1 per hour) or paid ($15 per hour) participation in accordance with a protocol approved by the Duke University Medical Center Institutional Review Board. The study length was approximately 90 min, preceded by 1 hr of preparation.

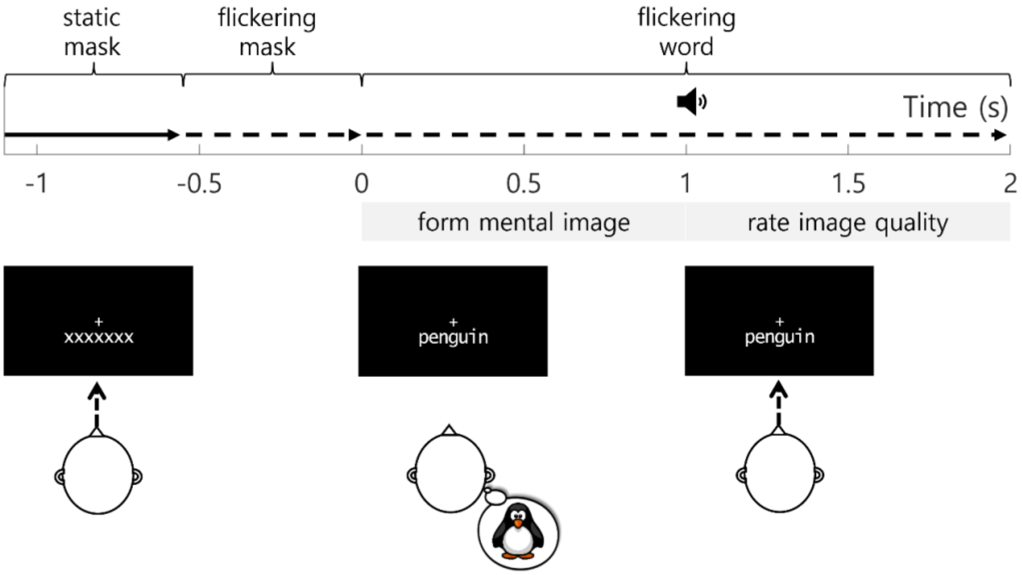

Figure 1: Sequence of events over the course of a word stimulus trial. Participants were presented with a mask, which was static for half of the time and flickering for the other half. This was followed by a flickering object-word stimulus that was presented for 2 s and flickered during the entire presentation. Participants were tasked with forming a mental image of the object and, after hearing a tone, rating the quality of the mental image.

2.2.2 Stimuli and procedure

The experiment was conducted in a dimly lit, electrically shielded room in which participants were seated 80 cm in front of a 24-inch stimulus presentation monitor (144 Hz refresh rate). Over the entire experimental session, participants completed an encoding phase, consisting of 600 trials, and a retrieval phase, consisting of 900 trials, with a 5-min break in between. In both the encoding and retrieval phases, participants were instructed to continuously fixate on a white cross present in the middle of a black screen. Each trial began with a static mask stimulus, which consisted of a row of 5-7 lowercase Xs, presented just below the fixation cross for 555.6 ms. This was followed immediately by the same mask stimulus presented flickering at 18 Hz, with 4 frames (27.8 ms) on and 4 frames off, for another 555.6 ms. The flickering mask was then replaced by a flickering 5-7 letter word stimulus of an object (95% of trials) or a 5-7 letter non-word stimulus (5% of trials), which flickered at 18 Hz for a full 2 s. The word and non-word stimuli were presented using a monospaced font (Lucida Console, size 24). To maintain a consistent visual input from trial to trial, the stimuli were grouped so that all the 5-letter words would appear in a row, followed by a group of the 6-letter words, and then a group of the 7-letter words. There were equal numbers of 5-, 6-, and 7-letter words across all stimuli. The number of Xs in the mask stimulus were matched to the number of letters in each word or non-word stimulus on that trial and presented in the same font and size. This was done so that the low-level sensory stimulation of the individual visual stimuli would not change on each trial. Presentation of the stimuli was controlled using Presentation 20.1 Software (Neurobehavioral Systems, Inc., Berkeley, CA). The encoding phase was broken up into 5 blocks of 120 trials each, and participants were able to determine the length of their breaks between blocks, with the entire encoding phase taking ~35 min to complete.

In terms of task, on trials in which a word was presented, participants were instructed to form a mental image of the word (image-generation period), adding as much imagery detail as possible. After 1 s, they heard a tone and had the remaining 1 s in the trial to rate the vividness of the image they had formed on a scale of 1 to 4, with 1 indicating poor/no image, 2 indicating fair image, 3 indicating good image, and 4 indicating excellent image (vividness-rating period). They were instructed to respond as quickly and accurately as possible after the tone on a keyboard using their left hand. To ensure that participants were rating the quality of the image they formed and not other features of the words, we gave the following examples: "A button response of 1 will mean you formed a very poor image or no image at all. If, for example, the word was "carburetor" and you couldn't really picture what that would look like, you would rate that image as a 1. If the word was bicycle, and you were able to imagine only the shape of the bicycle, you would rate that image as "ok", which is a 2. If you were able to imagine the pedals and wheels, you would rate that image as "good", or a 3. If you were able to imagine the bicycle in detail, for example, the color or a basket, you would rate that image as "excellent", or a 4. On trials in which a non-word stimulus was presented, participants were instructed to just press the space bar as quickly as possible. These catch trials were included to ensure that participants were attending during the presentation of the mask stimulus and could respond quickly as soon as the mask was replaced with the non-word stimulus.

The surprise retrieval phase was broken up into 5 blocks of 180 trials each and took a total of ~50 min to complete. Once again, participants were able to determine the length of their breaks in between each block. In this phase, all 570 words from the encoding phase were presented again, along with an additional 285 new words, as well as 45 new non-words for catch trials (5% of total). Each word was presented for 2 s and followed by a 1.1 s inter-trial interval. On trials in which a word was presented, participants were instructed to determine whether the word was old or new and rate their confidence of that response from 1, indicating definitely new, to 6, indicating definitely old, as quickly and accurately as possible. On trials in which a non-word stimulus was presented, participants were again instructed to press the space bar as quickly as possible. Responses were made on a keyboard using their left hand. There was no tone during the retrieval phase, so participants had a full 2 s to make their response.

2.2.3 Behavioral data and analysis

Overall memory performance was evaluated by comparing the hit rate and false alarm rate using a paired sample t-test. All accurate judgments were categorized as hits for old items and correct rejections for new items, regardless of confidence level. Similarly, all inaccurate judgments were categorized as misses for old items and false alarms for new items, regardless of confidence level. Mental imagery was evaluated behaviorally based on the vividness-rating reaction time (RT) at encoding and on subsequent memory for the word. The RTs are relative to the onset of the word stimuli. To create two well-separated levels of image vividness that also had sufficient and nearly equal numbers of trials, we binned trials into a *High Vividness* (*HighViv*) level, which included items rated at the highest vividness rating (4), and a *Low Vividness* (*LowViv*) level, consisting of trials with the two lowest vividness ratings (1 and 2). We compared the word stimuli within these two categories with regard to frequency of use

($t(20) = 1.01$, $p > .05$) and imageability ($t(20) = 1.12$, $p > .05$) and found no significant differences. The percent of items subsequently remembered for these two categories were compared using paired sample t-tests. Additionally, the vividness-rating RTs at encoding for the subsequently remembered items within these two categories (*HighVivRem* and *LowVivRem*) were compared using paired-sample t-tests. Trials with no behavioral responses were excluded from analysis. There were not enough forgotten trials to compare high- and low-vividness within this category (see **Table 1** for the trial counts of each condition). However, our main interest was in comparing the mechanisms by which high- versus low-vividness items are successfully encoded into episodic memory.

Table 1: Trial numbers per condition.

Trial Type	Minimum	Median	Maximum	Mean
Poor	7	39	104	49
Fair	16	93	158	91
Good	36	108	186	105
Excellent	24	126	340	151
LowVivRem	14	103	205	112
HighVivRem	18	108	293	133
LowVivForg	2	25	81	29
HighVivForg	2	8	62	18

2.2.4 EEG data acquisition and preprocessing

Online EEG data were recorded across both the encoding and retrieval phases from a custom, 64-channel, extended-coverage cap (Woldorff et al., 2002) with active electrodes (actiCAP, Brain Products GmbH) and an online right-mastoid reference. The impedances of the ground and mastoid electrodes were maintained below 5 kOhms, and the remaining electrodes were maintained below 15 kOhms. Data were digitized at a rate of 500 Hz per channel, with a three-stage cascaded integrator low-pass comb filter with a 130 Hz corner frequency. To monitor for blinks and horizontal eye movements, one electrode positioned below the left eye was used for the vertical electrooculogram (EOG) channel and two electrodes lateral to the outer canthus of each eye were used to compute the horizontal EOG channel. Offline, the EEG data were filtered using a 40 Hz low-pass filter, downsampled to 250 Hz, and then filtered using a 0.1 Hz high-pass causal FIR filter. Additionally, the data were re-referenced to the algebraic average of the left and right mastoid electrodes. Channels that appeared excessively noisy during data collection were interpolated using a spherical spline procedure (Perrin et al., 1989).

The EEG data were epoched from -2750 to 3750 ms, relative to the presentation of the word or non-word stimuli, to allow sufficient buffer zones on the ends for the time-frequency analysis. Additionally, the data were baseline-corrected based on the -200 to 0 ms pre-stimulus period, during which time the mask was flickering at 18 Hz. To detect eyeblinks occurring near the onset of the stimulus, which could influence the initiation of the neural processing cascade, the data were submitted to an algorithm using a 150-ms wide window moving across the epoch from -100 to 300 ms in 50-ms steps. Epochs with peak-to-peak voltage differences exceeding 48 μV in the vertical EOG channel were marked for rejection from the analysis. A copy of the EEG data was epoched from –1100 to 2000 ms, relative to the presentation of the word or non-word stimuli, to avoid overlapping trials. This copy was submitted to an infomax independent component analysis, and the resulting component weights were transferred back to the original data set. Ocular components of the independent component (IC) analysis reflecting eyeblinks were identified via visual inspection and removed from the data (at most 4 ICs per participant).

To detect horizontal eye movements, data were submitted to an algorithm that used a 150-ms wide window moving across the epoch from -100 to 2000 ms in 50-ms steps. Epochs with peak-to-peak voltage differences exceeding 24 μV in the vertical EOG channel, corresponding to approximately 1.5° of movement, were marked for rejection. Additional data-cleaning procedures were then performed. To remove high-amplitude noise or excess muscle activity, if three or fewer electrodes (excluding the vertical and horizontal EOG channels) exceeded ±100 μV for one epoch, each of these electrodes were replaced using the spherical-spline interpolation procedure. If more than three electrodes exceeded the threshold, the epoch was marked for rejection from the analysis.

Ten participants were excluded due to >55% of trials being rejected, either because of poor behavioral performance (i.e., making responses prior to the onset of the tone or failing to respond; n = 2), poor EEG data quality (n = 5), or a combination of both (n = 3). This left 21 participants (12 female, mean age 22.4 years) in the final analyses. For the remaining participants, 30.5% of trials were excluded on average. The nonword-stimulus catch trials were not included in the final analysis. Data were preprocessed and analyzed in MATLAB using a combination of the EEGLAB (Delorme & Makeig, 2004), ERPLAB (Lopez-Calderon & Luck, 2014), and FieldTrip (Oostenveld et al., 2011) toolboxes. The EEG cap featured a modified 10-10, equidistant electrode montage with extended inferior occipital coverage (Woldorff et al., 2002). We report electrode sites based on standard 10-10 electrode names if the electrode in our montage was within 5 mm of the corresponding 10-10 site. If the electrodes were 5-10 mm from the 10-10 site, the name has a prime appended to it. A subscript 'a' means that the electrode was 10-15 mm anterior to the listed 10-10 site, and a subscript 'p' means that the electrode was 10-15 mm posterior to the listed 10-10 site. No electrodes were further than ~.5 cm from their closest standard 10-10 site.

2.2.5 EEG and ERP analysis

Frequency decomposition of the EEG was performed using multitaper methods based on discrete prolate spheroidal sequences to estimate the power in logarithmically spaced frequencies from 3 to 40 Hz. The window widths for the tapers were 3 cycles for 3 Hz, 4 cycles for 4–7 Hz, 5 cycles for 8–14 Hz, 7 cycles for 15–20 Hz, and 10 cycles for 21–40 Hz. Spectral smoothing through multitapers was specified as $5 \times \log_{10}$ of each frequency. A decibel conversion was performed to normalize and baseline the data relative to the static period during the presentation of the mask stimulus (from -848 to -600 ms relative to the word stimulus onset).

The steady-state visual evoked response was calculated as the average magnitude of the oscillatory activity between 17 and 19 Hz across electrodes over occipital channels: Oz, O1′, O2′, PO3′, PO4′, PO7′, and PO8′. We selected the electrodes for the SSVEP analysis based on previous studies that have shown the SSVEP is observed over medial occipital sites, around Oz (for review, see Norcia et al., 2015), which was the scalp region where the SSVEPs in the current study numerically had their highest power. This measure served as an index of the direction of attention, with an increase in SSVEP power corresponding to increased externally-directed attention to the driving flickering stimuli and a decrease in SSVEP power corresponding to increased internally-directed attention and away from the flickering stimuli. To validate its use as an index of both externally- and internally-directed attention, SSVEP power data were submitted to a one-way rANOVA with three levels reflecting the three different time periods over the course of a trial: flickering-mask period (baseline), image-generation period, and vividness-rating period. The flickering-mask period was averaged from -555.6 to 0 ms relative to the onset of the word stimulus, reflecting the pre-stimulus flickering of the mask stimulus, in which participants were attending to the mask stimulus in anticipation of the word onset. The image-generation period was derived from the average magnitude from 0 to 1000 ms, covering the entire period in which participants were attending internally to form the mental image. The vividness-rating period was averaged from 1000 to 2000 ms, during which participants were attending externally to rate the quality of the mental image. We expected the SSVEP power to decrease while participants' attention was directed internally, away from the flickering stimulus, to form the mental image. After validating the SSVEP, we evaluated the attention-related processes during the image-generation period for subsequently remembered items. Mean SSVEP power data were submitted to a 2 (vividness: *HighVivRem*/*LowVivRem*) × 5 (time: 100-300 ms/300-500 ms/500-700 ms/700-900 ms,/900-1100 ms) repeated-measures analysis of variance (rANOVA) in 200 ms time bins. The first time bin starts at 100 ms to account for time spent perceiving the word. Post-hoc paired sample t-tests were performed to identify the time bins that significantly differed between conditions.

For the ERP analysis, we examined the Dm effect by selectively averaging trials time-locked to the onset of the word stimuli at encoding as a function of subsequent memory (Remembered vs. Forgotten). Based on previous literature, we selected a cluster of electrodes centered on electrodes Cz and CPz (Luck, 2014), including Cz, C1a, C2a, CPz, CP1′, CP2′, C1p, and C2p. Mean amplitude data were submitted to a 2 (memory: Remembered/Forgotten) × 5 (time: 400-500 ms/500-600 ms/600-700 ms/700-800 ms/800-900 ms) rANOVA to identify the Dm effect in 100 ms time bins. Post-hoc paired sample t-tests were conducted to identify the time bins in which the two conditions differed significantly. Then, to compare the encoding-related processes reflected by the Dm based on vividness, mean amplitude data of the remember-minus-forgotten difference waves were submitted to a 2 (vividness: *HighVivRem-minus-Forg*/*LowVivRem-minus-Forg*) × 5 (time: 400-500 ms/500-600 ms/600-700 ms/700-800/800-900 ms) rANOVA. Again, where the ANOVAs showed significant interactions, specific contrasts using post-hoc paired sample t-tests were conducted.

2.3 Results

2.3.1 Behavioral results

Overall memory performance at retrieval was well above chance with a mean hit rate of 82.9% (*SD* = 10.8) and false alarm rate of 30.2% (*SD* = 16.5), t(20) = 12.54, $p < .001$, *d* = 2.74. The data showed higher subsequent memory for the high-vividness items (*HighViv*; *M* = 88.9%, *SD* = 6.7%) in comparison to the low-vividness items (*LowViv*; *M* = 80.0%, *SD* = 10.5%), *t*(20) = 5.21, $p < .001$, *d* = 1.14 (**Fig 2A**), which were still remembered substantially higher than chance, *t*(20) = 12.21, $p < .001$, *d* = 2.67. These results indicate that forming more vivid mental images facilitated better encoding of those items for later retrieval.

To behaviorally assess the time spent at encoding forming the subsequently remembered mental images, we compared the vividness-rating RTs relative to the flickering-word onset time. Participants displayed faster RTs at encoding for the *HighVivRem* items (*M* = 1464 ms, *SD* = 86) compared to the *LowVivRem* items (*M* = 1519 ms, *SD* = 98), *t*(20) = 4.13, $p < .001$, *d* = .90 (**Fig 2B**). These results suggest that, for the successfully encoded items (those later remembered), participants spent less time at encoding forming the mental image for the items they rated as having excellent vividness, presumably because those items were easier and thus faster to imagine.

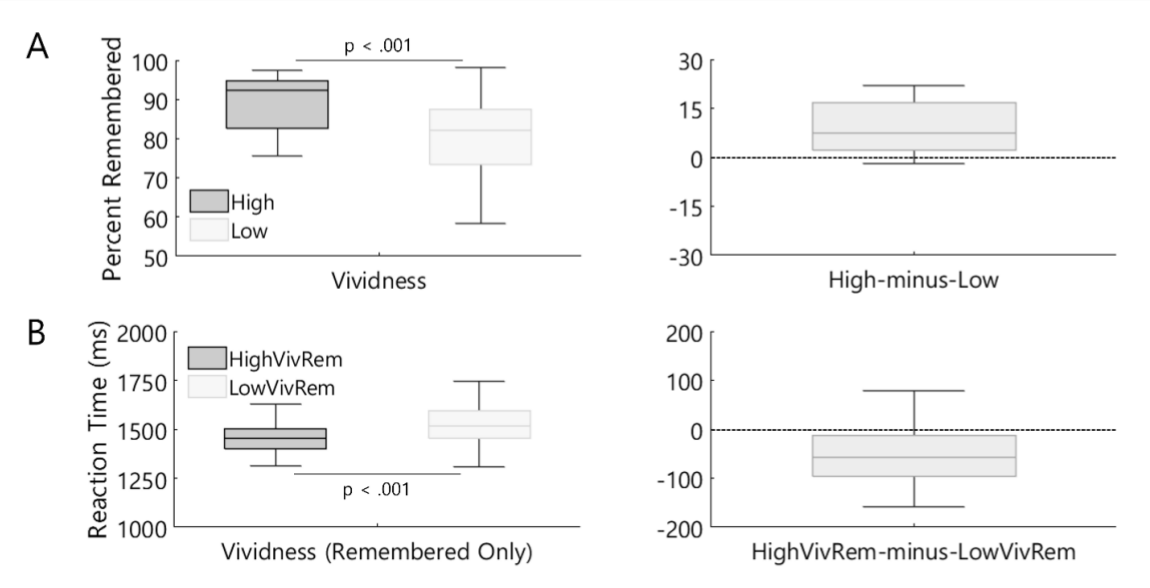

Figure 2: Behavioral results. A) The left panel shows the mean and distribution for the percent of items remembered that were rated as high-vividness compared to low-vividness. The right panel shows the within-subject difference between the high- and low-vividness categories. Results showed that there was better subsequent memory for high-vividness items. B) The left panel shows the mean and distribution for the vividness-rating reaction times at encoding between the subsequently remembered high-vividness compared to low-vividness items. The right panel shows the within-subject RT difference between the two categories. Participants were faster to make vividness ratings for high-vividness items.

2.3.2 Goal 1: Using SSVEPs to track shifts between externally- and internally-directed attention

The first goal of this study was to investigate the use of SSVEPs as an index of the direction of attention (external vs. internal). We hypothesized that after reading the flickering word stimulus, participants would direct their attention internally to form the mental image of the item, resulting in a decrease of the externally-driven SSVEP. The SSVEP would then return to pre-imagery baseline once participants heard the tone and re-directed attention to the visual screen to rate the vividness of the mental image. To test this hypothesis, we controlled for memory and evaluated the time-course of all subsequently remembered trials by comparing the SSVEP amplitude across the flickering-mask period (-555.6 to 0 ms), the image-generation period (0 to 1000 ms), and the vividness-rating period (1000 to 2000 ms). SSVEP power data were submitted to a one-way rANOVA with three time-period levels: flickering-mask period, image-generation period, and vividness-rating period. Note that a flickering stimulus was present during these three periods so changes in SSVEP power can be safely attributed to shifts between externally- and internally-directed attention rather than to perceptual changes.

We observed a significant effect of time-period, $F(2, 40) = 16.44$, $p < .001$, $n_p^2 = .45$ (**Fig 3A**). Post-hoc paired sample t-tests showed that SSVEP power was significantly reduced, $t(20) = 5.33$, $p < .001$, $d = 1.16$, from the externally-oriented, flickering-mask period ($M = .51$, $SD = .73$), to the internally-oriented, image-generation period ($M = -.03$, $SD = .67$), and then it significantly increased, $t(20) = -4.95$, $p < .001$, $d = -1.08$, to the externally-oriented, vividness-rating period ($M = .76$, $SD = 1.24$). There was no significant difference between the flickering-mask and vividness-rating periods, $t(20) = -1.62$, $p > .05$, $d = -.35$.

In sum, consistent with our first hypothesis, the results validate the use of SSVEP power as a means to index shifts between externally- and internally-directed attention: (1) when participants directed attention externally during the flickering-mask period, SSVEP power was high, (2) when they directed attention internally during the image-generation period, SSVEP power decreased significantly, and (3) finally, when they directed their attention externally again during the vividness-rating period, SSVEP power increased reliably, returning to baseline.

2.3.3 Goal 2: Investigate the relationship between SSVEPs and the quality of mental images

For our second goal, we tested two alternative hypotheses. According to one hypothesis, more intense and/or longer internally-directed attention would lead to higher image vividness, whereas according to the other hypothesis, more intense and/or longer internally-directed attention would be necessary when images were more difficult to generate. To avoid confounding the effects of imagery with the effects of successful encoding processes, these hypotheses were tested using only subsequently remembered items. The former hypothesis predicts that the SSVEP decrease during the image-generation period should be greater and/or more sustained for *HighVivRem* compared to *LowVivRem* items, whereas the latter hypothesis predicts the opposite result. SSVEP power data were submitted to a 2 × 5 rANOVA, with a two-level factor of vividness (*HighVivRem*/*LowVivRem*) and a five-level factor of time (100-300 ms/300-500 ms/500-700 ms/700-900 ms/900-1100 ms). **Figure 3B** displays the time-course of SSVEP power for the *HighVivRem* and *LowVivRem* items, and **Figure 5A** displays the mean power and within-subject standard error for each time bin. **Table 2** displays means and standard deviations for the five time windows during the image-generation period.

These analyses indicated that there was no main effect of imagery vividness in this analysis, $F(1, 20) = 2.50$, $p = .13$, $n_p^2 = .11$, indicating no significant difference in the mean SSVEP power integrated across the entire examined time period. There was, however, a main effect of time, $F(4, 80) = 13.98$, $p < .001$, $n_p^2 = .41$, indicating that SSVEP power was modulated over the course of the trial, as shown in both **Figures 3A** and **3B**. Most importantly, there was an interaction between vividness and time, $F(4, 80) = 4.78$, $p = .002$, $n_p^2 = .19$. Post-hoc paired sample t-tests comparing the *HighVivRem* and *LowVivRem* items over the course of the trial showed significant differences during the 700-900 ms, $t(20) = 2.51$, $p = .02$, $d = .55$, and 900-1100 ms time bins, $t(20) = 2.69$, $p = .01$, $d = .59$.

These results indicate that SSVEP power was reduced for a longer time for the *LowVivRem* compared to *HighVivRem* items. This finding is consistent with the alternative hypothesis that the shift to internally-directed attention is more intense and/or longer for *LowVivRem* than *HighVivRem* items, presumably because the mental images were harder to form, thus fitting with the second hypothesis above. It is worth noting that the vividness-rating RTs were also slower for *LowVivRem* than *HighVivRem* items, providing converging evidence for the second hypothesis.

Table 2: SSVEP mean power (dB) and standard deviation across time.

	HighVivRem	LowVivRem
100 – 300 ms	-.11 (.46)	-.19 (.58)
300 – 500 ms	-.45 (.57)	-.51 (.73)
500 – 700 ms	-.21 (.76)	-.35 (.83)

700 – 900 ms	.32 (1.19)	-.08 (1.03)
900 – 1100 ms	.70 (1.37)	.26 (1.10)

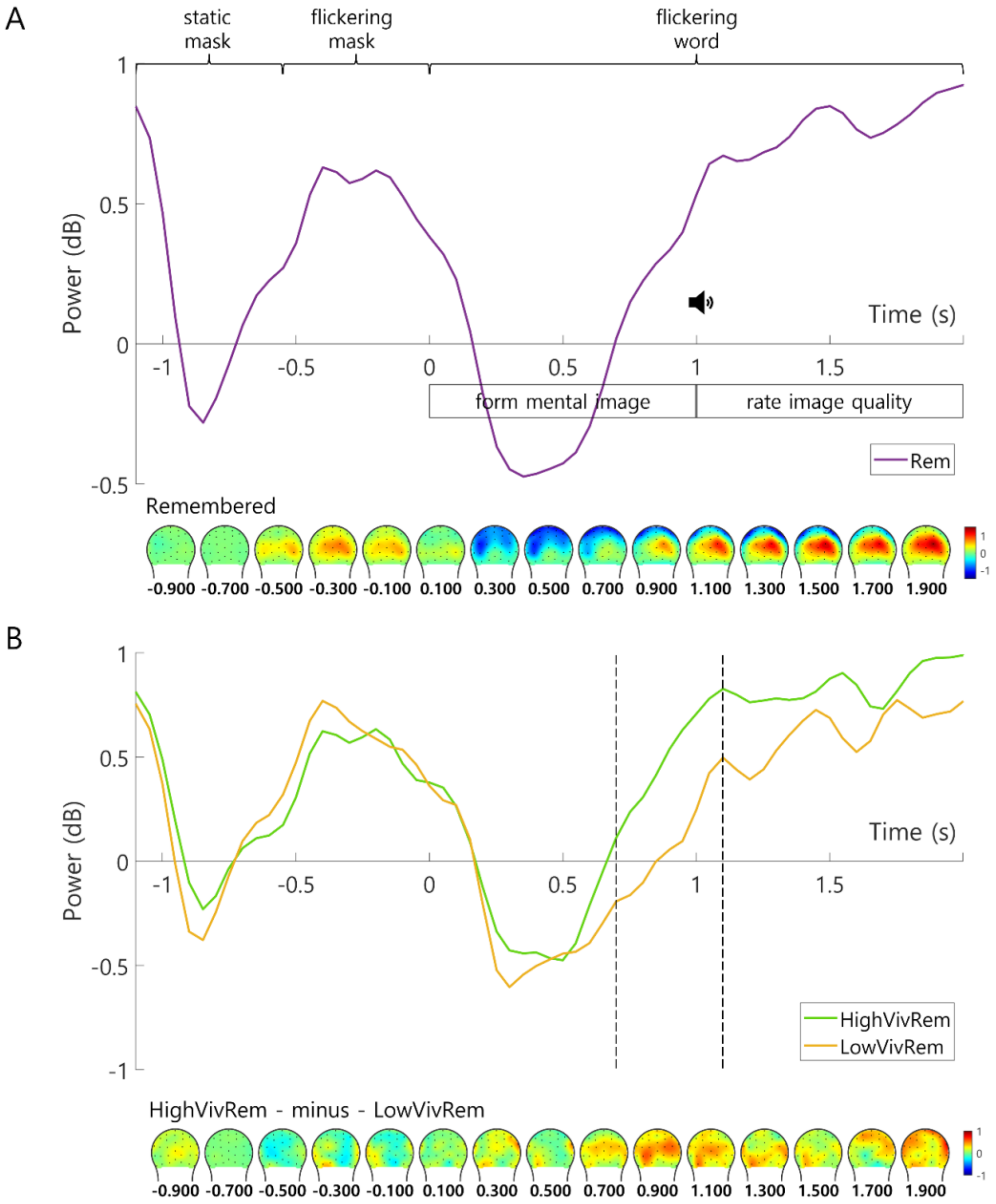

Figure 3: SSVEP results. A) Timelock-averaged occipital SSVEP power plotted over the time course of a trial, with the onset of the flickering word stimulus at time 0. During the flickering-mask period (-555 to 0 ms) and the vividness-rating period (1000 to 2000 ms), SSVEP power was high as participants directed their attention externally

toward the flickering visual stimulus on the screen. During the image-generation period in between (0 to 1000 ms), however, there was a substantial decrease in SSVEP power as participants directed their attention internally to form the mental image, after which it returned to a high level as attention was redirected externally back to the screen during the vividness-rating period. The topographic plots show the time course of the trial in 200 ms time bins, with each bin labeled with the middle time point in each 200 ms period. (B) Timelock-averaged occipital SSVEP power across the time course of a trial, plotted separately for the subsequently remembered high-vividness and low-vividness items. The SSVEP power returned more slowly to baseline when forming low-vividness mental images, consistent with participants being slower to redirect their attention externally. The dashed lines represent the time-periods in which a significant difference was observed. The topographic plots show the difference between the high- and low-vividness trials across time, plotted in 200 ms time bins, labeled again with the middle time point of each bin displayed.

2.3.4 Goal 3: Examine the influence of image vividness on the Dm effect

Beside imagery, a major factor contributing to successful encoding is thought to be related to conceptual processing (Craik & Lockhart, 1972), which in ERP studies, has been often linked to the Dm ERP effect (Otten & Rugg, 2001; Paller et al., 1987). Thus, it is possible that one of the reasons why *LowViv* items could be subsequently remembered despite the poor images that were generated for them is because they received greater conceptual processing, perhaps due to the difficulty and time required to generate the images. If so, the Dm effect should be greater or more sustained for *LowViv* than *HighViv* items. To examine differences in the encoding-related processes for the *HighVivRem* and *LowVivRem* items, Dm amplitude data during the image-generation period were submitted to a 2 (memory: remembered/forgotten) × 5 rANOVA (time: 400-500 ms/500-600 ms/600-700 ms/700-800 ms/800-900 ms). **Table 3A** displays the means and standard deviations for each condition and the results of the t-tests for each time bin.

First, we identified the Dm by comparing subsequently remembered to forgotten items. Results showed a main effect of memory, $F(1, 20) = 13.46$, $p = .001$, $n_p^2 = .40$ and a main effect of time, $F(4, 80) = 2.55$, $p < .05$, $n_p^2 = .11$, with no interaction of these two factors, $F(4, 80) = .70$, $p > .05$, $n_p^2 = .03$. Post-hoc paired sample t-tests showed significant differences between subsequently remembered and forgotten items in each time bin from 400 to 900 ms (**Fig 4A**). After identifying the Dm *main* effect for later remembered versus later forgotten items, we compared amplitudes for the *HighVivRem-minus-*Forg and *LowVivRem-minus-*Forg Dm difference waves to investigate differences in encoding processes for high- versus low-vividness items. **Table 3B** displays the means and standard deviations, as well as the results of the t-tests for each time bin. Results showed no main effect of vividness, $F(1, 20) = 1.25$, $p > .05$, $n_p^2 = .06$, but a main effect of time, $F(4, 80) = 2.53$, $p < .05$, $n_p^2 = .11$. Most importantly, however, the results showed a significant interaction of time and vividness rating, $F(4, 80) = 6.87$, $p < .001$, $n_p^2 = .26$ (**Fig 4B**), indicating the Dm effect did not follow the same time course for each vividness condition. **Figure 5B** displays the mean amplitude and within-subject standard error for each time bin. Post-hoc paired sample t-tests showed significant differences between the *HighVivRem-minus-*Forg and *LowVivRem-minus-*Forg Dm difference waves from 700 to 900 ms. These results suggest that participants were able to successfully encode the HighViv items into episodic memory more quickly, while the *LowViv* items required additional or more sustained conceptual processing for successful subsequent retrieval.

Table 3: Post-hoc paired sample t-tests for the Dm comparisons in each time window.

A) Remembered vs. Forgotten

	Rem Mean (SD)	Forg Mean (SD)	t	df	p	d
400 – 500 ms	.93 (3.42)	-.16 (2.86)	3.68	20	.001	80
500 – 600 ms	2.16 (3.44)	.75 (3.01)	4.10	20	<.001	.89
600 – 700 ms	2.21 (2.96)	.93 (2.44)	3.40	20	.003	.74
700 – 800 ms	2.03 (2.34)	.78 (2.16)	3.33	20	.003	.73
800 – 900 ms	1.49 (2.07)	.46 (2.25)	2.33	20	.03	.51

B) HighVivRem-minus-Forg vs. LowVivRem-minus-Forg

	HighVivRem-*minus-Forg* Mean (SD)	*Low*VivRem-*minus-Forg* Mean (SD)	t	df	p	d
400 – 500 ms	.99 (3.28)	.77 (3.75)	.60	20	.56	.13
500 – 600 ms	2.20 (3.58)	2.29 (3.77)	-.25	20	.80	-.06
600 – 700 ms	2.10 (3.15)	2.64 (3.46)	-1.13	20	.27	-.25
700 – 800 ms	1.59 (2.48)	2.74 (2.87)	-2.42	20	.03	-.53
800 – 900 ms	1.02 (2.00)	2.22 (2.83)	-2.48	20	.02	-.54

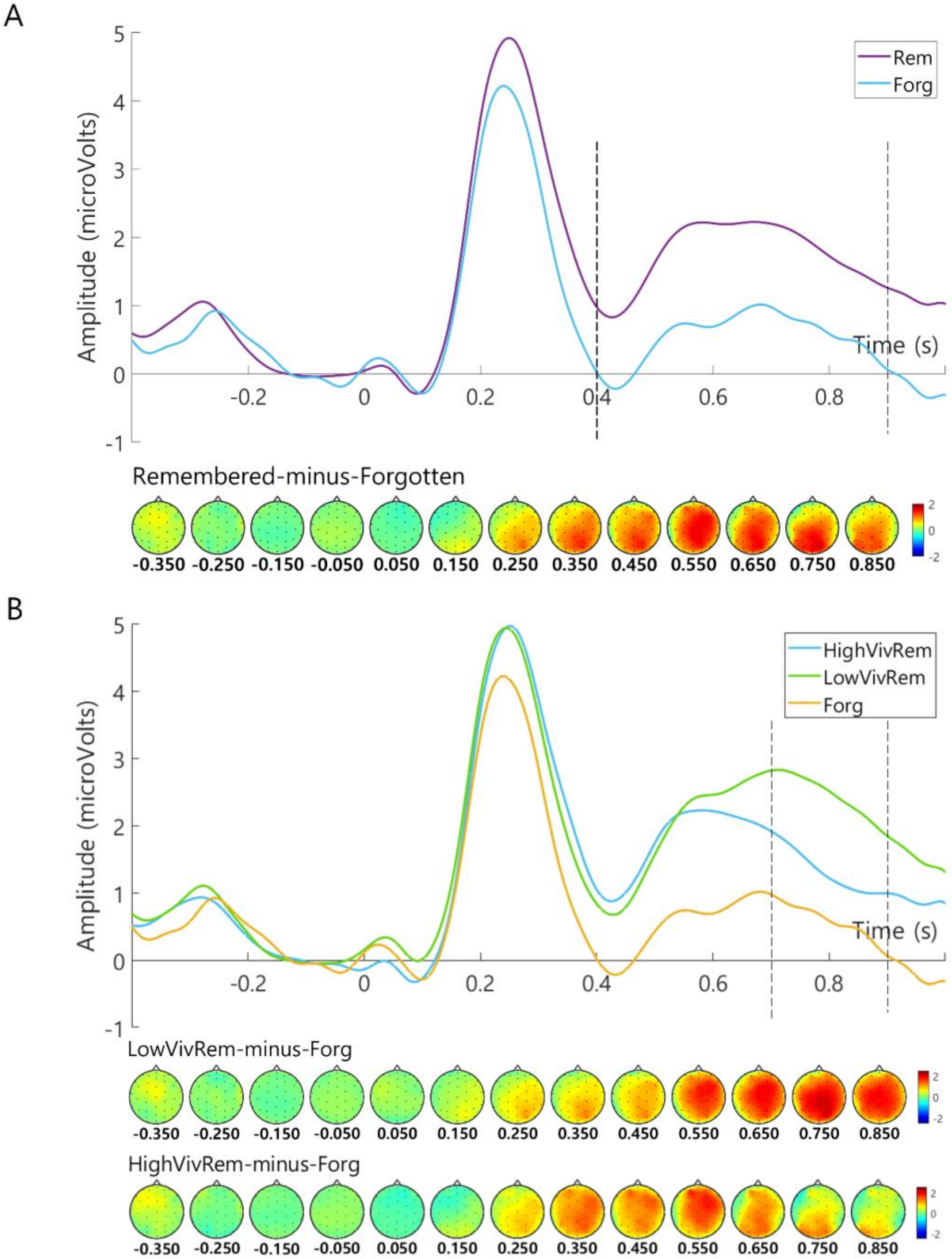

Figure 4: Dm results. A) The Dm difference at encoding for subsequently remembered vs. subsequently forgotten items was observed over centro-parietal regions starting at around 400 ms. The dashed lines represent the time-periods in which a significant difference was observed. The topographic plots show the

difference between the subsequently remembered and forgotten trials plotted in 100 ms time bins, with the middle time of each bin displayed. B) The Dm amplitudes were compared between the high-vividness subsequently remembered items and low-vividness subsequently remembered items. Results showed that the Dm effect persisted longer for the low-vividness items, with the dashed lines delimiting the time-periods in which significant differences were observed. The topographic plots show the remembered minus forgotten differences for both the low- and high-vividness items over time in 100 ms time bins, with the middle time displayed.

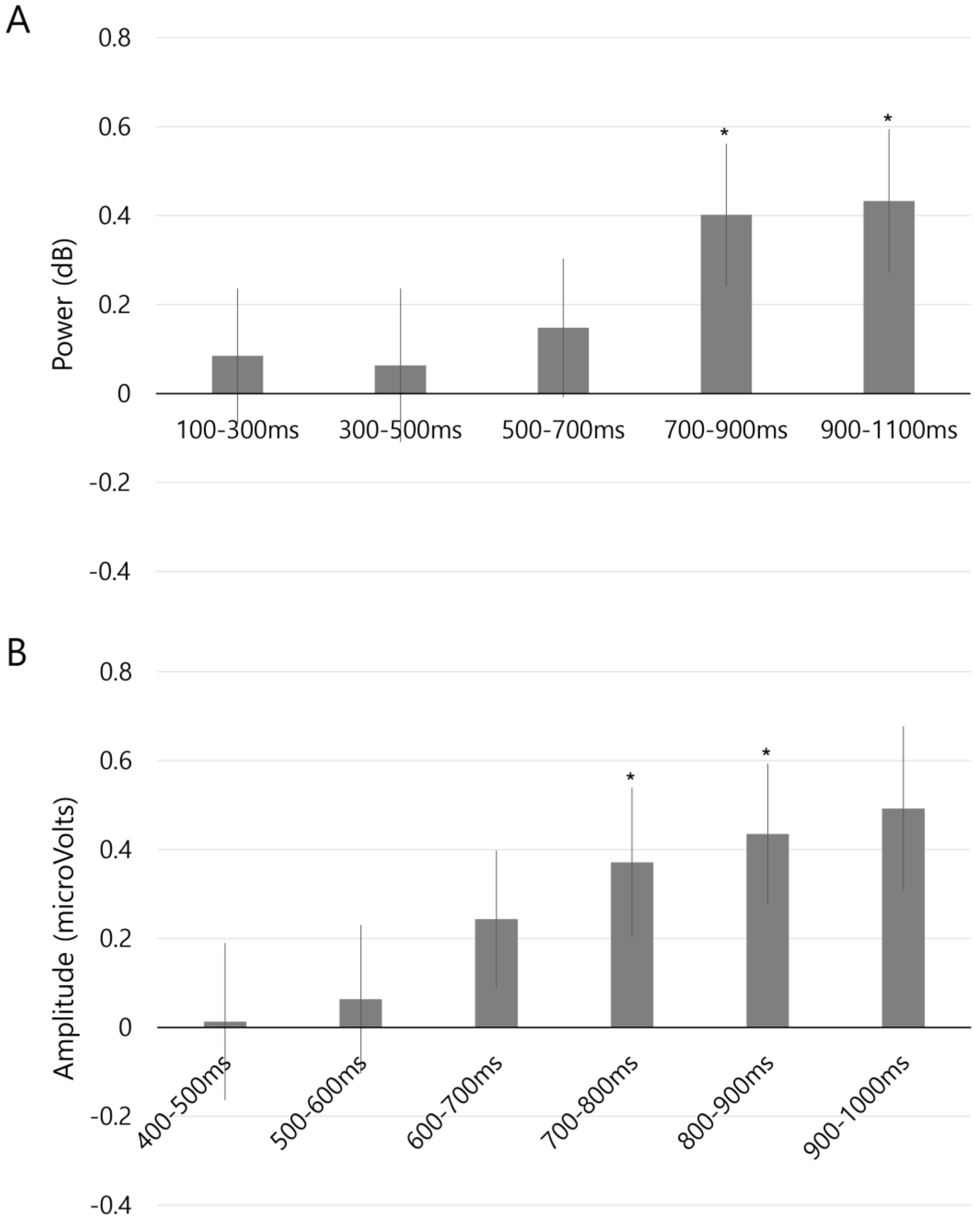

Figure 5: Comparisons of within-subject differences between conditions at each time window for the main SSVEP and Dm analyses. A) The HighVivRem minus LowVivRem calculation for SSVEP power within each time bin, with error bars indicating within-subject standard error. The asterisks indicate $p < .05$. B) The

HighVivRem minus LowVivRem calculation for Dm amplitude within each time bin with error bars indicating within-subject standard error. The asterisks indicate $p < .05$.

2.4 Discussion

Using a visual mental imagery task in combination with a subsequent-memory paradigm, we investigated the neural mechanisms supporting the successful encoding of internally-generated information into episodic memory and the modulation of those neural mechanisms by the quality of the information, which was indexed by the self-reported vividness of mental images in this paradigm. Participants were presented with a series of flickering object-word stimuli and instructed to form a visual mental image of the object referent for each word and then rate the quality of the image in terms of its vividness. In our analyses, we focused on the processing at encoding of high- versus low-vividness items that were subsequently remembered.

Our behavioral results were consistent with previous research and theories. In line with prior studies (D'Angiulli et al., 2013b; De Beni & Pazzaglia, 1995; Marcotti & St Jacques, 2018; Reisberg et al., 1986), we observed improved subsequent memory for high-vividness items – i.e., those where participants were able to form vivid visual mental images -- as compared to low-vividness items. Our finding of shorter vividness rating RTs for high- versus low-vividness items are in line with D'Angulli and colleagues' (2013) hypothesis — based on multi-trace memory theory (Moscovitch et al., 2005) — that vividness ratings reflect the availability of multiple sensory traces in long-term memory, and therefore, faster image generation is observed for higher-vividness items (D'Angiulli & Reeves, 2002).

The neural results showed three main findings. First, we observed reduced SSVEP power as subjects directed attention internally to form a mental image of the word's referent. Second, objects rated as low-vividness showed a slower return of SSVEP power to pre-imagery baseline compared to high-vividness items. In line with the behavioral vividness-rating RT results, this suggests that longer internally-directed attention was needed to generate low-vividness images. Finally, we observed a more sustained Dm for the subsequently remembered low-vividness items compared to subsequently remembered high-vividness ones, suggesting additional conceptual processing was necessary to compensate for the low vividness of the mental image and still remember the item. These three findings are discussed in separate sections below.

2.4.1 SSVEPs can index shifts between externally- and internally-directed attention

Most SSVEP studies have used this measure to index externally-directed attention. For example, SSVEPs have been used to track visuospatial attention (Andersen et al., 2008, 2011; Morgan et al., 1996), sustained attention (Silberstein et al., 1990), working memory (Ellis et al., 2006; Silberstein et al., 2001; Van Rooy et al., 2001), and emotional stimulus processing (Hindi Attar et al., 2010; Kemp et al., 2002, 2004). In a novel use of this technique here, we employed SSVEPs to track internally-directed attention in a visual mental imagery task. We hypothesized that power would be highest during the flickering-mask period (externally-directed attention), would drop during the image-generation period (internally-directed attention), and then would return to baseline as attention was redirected to the screen during the vividness-rating period (externally-directed attention). The results confirmed this hypothesis, indicating SSVEPs can be used to track shifts between externally- and internally-directed attention during cognitive tasks. These results are in line with a recent study published by Kritzman et al., (2022), which used the SSVEP as an index of internally-directed attention in an interoceptive processing task. Their results showed that SSVEP magnitude and phase synchronization decreased when participants directed their attention toward their heartbeats.

Our finding has implications for the use of SSVEPs in research on the cognitive and neural mechanisms of shifts between externally- and internally-directed attention, as well as studies on the impact of these shifts on other cognitive processes. For example, one fruitful line of research would be to use SSVEPs to examine lapses in sustained attention, which may reflect both external distractions from the environment or from the person's own thoughts, as in the case of mind-wandering (deBettencourt et al., 2018; Stawarczyk, Majerus, Maj, et al., 2011; Unsworth & McMillan, 2014; Unsworth & Robison, 2016). Additionally, the SSVEP technique can be effectively used to measure attention and memory processes that occur internally, such as the impact of visual imagery on subsequent memory, as in the current study.

2.4.2 SSVEP power returned to baseline more slowly for low- than high-vividness images

We tested two alternative hypotheses regarding the relationship between internally-directed attention and the quality of mental images. One hypothesis was that greater and/or longer internally-directed attention contributes to more vivid images, whereas the alternative hypothesis was that greater and/or longer internally-directed attention is required when images are difficult to form. Our second main neural finding was that a more prolonged dip in SSVEP power during the object imagery process was observed for low- compared to high-vividness remembered items. This finding is consistent with the alternative hypothesis, and it suggests that participants spent more time with attention directed internally as they tried to form the mental images of the low-vividness items.

This idea is also consistent with the vividness-rating RTs being longer for low- than high-vividness remembered items, providing converging evidence for the alternative hypothesis. Participants were not asked to press the vividness rating key as quickly as possible after they finished generating each image, so rating RTs provide only an indirect measure of the duration of the image-generation process. However, we would expect participants to be even faster at making the ratings for the high-vividness items if they did not have to wait for a tone, thereby increasing the difference in RTs between the high- and low-vividness items. Since participants were trying to generate vivid images, it is reasonable to infer that once they were satisfied with the quality of the mental image they generated, they began shifting to the task of rating the image more quickly, but when they were not satisfied with the image quality, they continued trying to improving their mental image and shifted to the rating task later. We were able to directly confirm that there were no differences between the items rated as high-vividness compared to those rated as low-vividness in terms of frequency of use or imageability of the words. However, further research is warranted to directly examine the role of other possible factors.

Increases in SSVEP power can be used to link externally-directed attention toward the flickering stimuli to specific brain regions, within the spatial resolution of EEG. In the current study, we observed SSVEP power over occipital cortex (**Fig. 3A**), consistent with externally-directed attention being focused on a central flickering visual stimulus (Andersen et al., 2011; Norcia et al., 2015). In contrast, decreases in SSVEP power suggest that a shift toward internally-directed attention occurred. However, the decrease in SSVEP power does not give us insight into the specific cognitive operation that was the focus of internally-directed attention or the specific brain regions mediating attention to these internal targets. Functional MRI (fMRI) studies have linked internally-directed attention during visual mental imagery to the default mode network (DMN), operating in collaboration with frontal areas (Ishai et al., 2000; Pearson, 2019a; Schlegel et al., 2013; Yomogida et al., 2004). Thus, a future combined EEG-fMRI study, may be useful to directly link the SSVEP power reduction to modulations of activity in the DMN and its interactions with frontal regions. Each of these areas could contribute differently to subsequent memory of internally-generated information.

2.4.3 The Dm was more sustained for low- vs. high-vividness remembered items

The Dm neural ERP effect showed a prolonged duration for the low-vividness versus high-vividness items that were later remembered. Previous research has shown that the Dm ERP is modulated by conceptual processing (for a review, see Friedman & Johnson Jr., 2000; Wagner et al., 1999). For example, enhanced Dm amplitude was observed for tasks requiring semantic decisions compared to non-semantic decisions (Paller et al., 1987). In the current study, the Dm effect was more sustained for low- than for high-vividness items. Taken together with the SSVEP results, this finding suggests that one of the factors contributing to later memory for the more poorly imagined items could be that they received greater higher-level conceptual processing.

This idea is consistent with the results of an early behavioral study (Wiseman & Neisser, 1974) in which participants viewed incomplete pictures, either providing a meaningful interpretation or just attending to the meaningless pictures. Results showed better recognition memory for the pictures that were given meaningful interpretations at encoding. Similarly, a study in which words and pictures were either named or categorized showed that pictures were later better remembered than words (picture-superiority effect) in the naming condition but equally well-remembered in the categorization condition (Vaidya & Gabrieli, 2000). The results of these studies suggest that conceptual processing can compensate for poorer imagery. Furthermore, a study comparing deep vs shallow encoding showed that deep encoding was associated with a larger and longer-lasting Dm(Guo et al., 2004)-. While our findings robustly show differences in Dm duration for low- vs high-vividness items that are later remembered, future studies are needed to directly investigate the compensatory strategies that may be employed when participants are unable to form a highly vivid visual mental image.

Our findings reveal important differences in the time-course for the processing of high- versus low-vividness items that are subsequently remembered. Not only did the low-vividness items require more time spent with attention directed internally (as reflected by a slower return to baseline from the dip in SSVEP power during the imagery process), but they also showed a prolonged Dm ERP effect, suggesting that there may have been additional higher-level conceptual processing for the successful encoding of these items that enabled them to be subsequently remembered. To further investigate the neuroanatomical underpinnings of such processes, future research using functional MRI could compare the perceptual versus conceptual representations for high- versus low-vividness items. Previous fMRI studies have used representational similarity analysis to investigate the different brain regions where visual and semantic representations predict perceptual memory, conceptual memory, or both (Davis et al., 2021). Although fMRI imaging measures would not be able to provide the temporal dynamics of the encoding-related processes revealed by the EEG/ERP effects presented here, they could offer insight into the specific neural regions activated at encoding that support subsequent memory for the low-vividness compared to high-vividness items.

2.4.4 Conclusion

In conclusion, this study shows that differences in the vividness of a mental image are related to changes in internally-directed attentional processes and encoding-related processes, as well as their time courses. When subjects encoded subsequently remembered images with low vividness, we observed a slower return of the SSVEP dip back to the pre-imagery baseline and a more sustained Dm ERP positivity, relative to subsequently remembered images that had high vividness. This pattern of results suggests that more sustained internally-directed attention, in conjunction with more prolonged encoding-related processing, is needed to successfully remember less salient mental representations.

3. Neural retrieval processes occur more rapidly for visual mental images that were previously encoded with high-vividness

3.1 Introduction

Imagine that you are studying for a test about DNA replication. You might facilitate your learning by generating a rich visual image of the key structures and processes, which you can then retrieve during the test. Our capacity to experience visual images of events or objects, in the absence of sensory stimulation, is known as “visual imagery” (Pearson, 2019b). The above example illustrates the fact that individuals can encode visual mental images and retrieve them to aid in performing a memory-dependent task (Legge et al., 2012; Maguire et al., 2003). While several studies have shown that visual mental imagery can improve memory performance (Bower, 1972; D’Angiulli et al., 2013b; Foley, 2012; Gjorgieva et al., 2022; Gupton & Frincke, 1970; McCauley et al., 1996; Mueller & Jablonski, 1970), there is relatively little research about the neural mechanisms whereby visual mental images enhance episodic memory.

The scientific study of imagery has explored the neural activations associated with the generation of visual mental images, as well as the modulation of these neural activations according to the ascribed vividness of imagery. Studies have shown that visual imagery generation depends on some of the regions that process visual information itself. Lower-level areas in visual cortex (Kosslyn and Thompson 2003; Lee et al. 2012; but see Spagna et al. 2021), higher-level visual areas (O’Craven & Kanwisher, 2000; Pearson et al., 2015), as well as regions in the temporal lobe (Koenig-Robert & Pearson, 2019; Naselaris et al., 2011) have all been implicated in the generation of visual imagery. Taken together, these findings support the idea that there is neural overlap between visual perceptual processes and visual imagery processes. However, there are also key differences between visual perception and imagery. The temporal dynamics of visual imagery processes are distinct from visual perceptual processes, evolving later in time (Dijkstra et al., 2018). Additionally, Yu and Postle (2021) found that internally-generated information is represented differently from typical working memory representations of visually perceived items, which are comprised from external sources. Importantly, visual mental imagery has been shown to improve long-term memory performance (Bower, 1972; Cornoldi & Paivio, 1982; D'Angiulli et al., 2013b; Foley, 2012; Gupton & Frincke, 1970; McCauley et al., 1996; Mueller & Jablonski, 1970). These unique features of visual mental imagery underscore the necessity of further investigations into the underlying neural processes, and in particular, its role in episodic memory.

One key factor to explore in this regard is vividness, a self-reported expression of the degree of richness and level of detail of a visual mental image (D'Angiulli & Reeves, 2007). Vividness has been found to be related to the amount of overlap in neural representation between imagery and perception in the visual and parietal cortices (Dijkstra, Bosch, & van Gerven, 2017). Visual mental images can vary greatly in terms of their vividness (Cui et al., 2007), and studies using functional magnetic resonance imaging (fMRI) have shown this variation to modulate neural activation in the precuneus, right parietal cortex, medial frontal cortex, and parts of early visual cortex (Dijkstra, Bosch, & van Gerven, 2017). Behaviorally, studies of visual imagery generation have observed faster vividness-rating reaction times (RTs) for more vivid items during the image generation period (D'Angiulli et al., 2013b; D'Angiulli & Reeves, 2002; Gjorgieva et al., 2022). One hypothesis put forth to explain the RT difference suggests that vividness-rating RTs are representative of the availability of multiple sensory traces in long-term memory (D'Angiulli et al., 2013b). Thereby, high-vividness mental images are generated more quickly because sensory traces are more readily available. In addition, studies have shown that more vivid mental images are better remembered (D'Angiulli et al., 2013b; De Beni & Pazzaglia, 1995; Gjorgieva et al., 2022; Marcotti & St Jacques, 2018; Reisberg et al., 1986; Tulving et al., 1965). A previously published paper by our group investigating the encoding of visual mental images found two main differences for those items rated as low vs. high vividness (Gjorgieva et al., 2022). First, we found that attention was directed internally during the image generation process, and the low-vividness items that were later remembered were characterized by a longer duration period of internally-directed attention during encoding. In addition, we observed a more sustained event-related-potential (ERP) difference due to memory (Dm) at encoding for subsequently remembered items, suggesting that low-vividness items that were subsequently remembered may have required additional conceptual processing at encoding to compensate for the poor imagery. Taken together, these studies indicate that visual mental imagery can vary in its richness and that this variation has an impact on processing speed and subsequent memory. However, relatively little is known about the neural mechanisms and the time-course by which images with different levels of vividness at encoding are retrieved from episodic memory.

At the electrophysiological level, episodic memory has most commonly been characterized by the parietal old/new effect, an event-related potential (ERP) with a positive deflection peaking between 400-800 ms over parietal cortex (Curran, 2000, 2004; Friedman & Johnson, 2000; Rugg & Curran, 2007; Wilding, 2000; Woodruff et al., 2006). The parietal old/new effect is measured during memory retrieval and has been shown to be modulated by the depth of processing at encoding (Rugg et al., 1998), as well as the amount (Vilberg et al., 2006; Vilberg & Rugg, 2009) and quality (MacLeod & Donaldson, 2017; Murray et al., 2015) of recollected information at retrieval.

In addition to the parietal ERP, studies have shown that both the amount and the timing of alpha-band EEG desynchronization (i.e., a decrease in the “strength” of the oscillatory activity between 8-12 Hz) are associated with the amount of memory retrieved for previously encoded words: improved memory is associated with a bigger and earlier increase in alpha desynchronization (i.e., a decrease in alpha-band power; Martín-Buro et al. 2020). In addition, higher desynchronization in both the alpha (8-12

Hz) and low-beta (12-20 Hz) frequency bands at retrieval has been associated with higher discrimination between previously encoded images and similar lure images (Karlsson et al., 2020) as well as with the fidelity of the information represented in the cortex (Griffiths et al., 2019). Taken together, these results support the idea that alpha and/or alpha/low-beta desynchronization may reflect the promotion of the information flow to the neural substrates that represent mnemonic content (Hanslmayr et al., 2012, 2016; Klimesch et al., 2007).

The main objective of the current study was to examine the neural processes associated with the retrieval of previously generated visual mental images, as well as how the vividness of those mental images (self-reported during image generation at encoding) can modulate retrieval processes. To do this, we employed a paradigm composed of two phases while we recorded the electroencephalographic (EEG) activity of human participants (**Fig 6**). In the first phase, participants were presented with a series of flickering object words and asked to form a mental image of the referent denoted by the word. On each trial, participants then rated the vividness of the mental image they had just formed. In the second phase, participants completed a surprise memory task. During the memory task, participants were presented with both old and new words and tasked with indicating whether the word was old (seen in the first phase) or new (not seen in the first phase) and rating their confidence in that judgment. This experimental paradigm thus allowed us to have a behavioral measure of vividness during encoding, as well as a measure of accuracy and subjective confidence at retrieval, while concurrent brain activity data was being recorded. The findings from the encoding phase were reported in a separate publication (Gjorgieva et al., 2022).

We investigated the retrieval of visual mental images by examining the magnitude of the parietal old/new ERP effect as well as the magnitude and latency of EEG alpha-band power changes. In line with previous research (Rugg & Curran, 2007), we expected a modulation of the parietal old/new effect by memory when comparing the activity elicited at retrieval by items subsequently remembered to new items that were correctly identified as new. Similarly, following the results of Martín-Buro et al. (2020), we expected that the amount of alpha desynchronization would be greater for successfully remembered items compared to correctly identified new items. To compare the retrieval of low- vs high-vividness items purely based on vividness, we controlled for memory accuracy and confidence by examining only the items successfully remembered with high confidence. We hypothesized that if high-vividness items were retrieved with increased or improved mnemonic information, we would observe an increased magnitude in the parietal old/new effect (Murray et al., 2015; Vilberg et al., 2006; Vilberg & Rugg, 2009). Additionally, we examined the role of alpha-band desynchronization in visual mental imagery retrieval. The amplitude (Griffiths et al., 2021; Martín-Buro et al., 2020) and timing of alpha desynchronization (Martín-Buro et al., 2020; Michelmann et al., 2016) have been proposed as indices of the accumulation of memory strength, so both are potential mechanisms that could support the behavioral advantage of vividly encoded imagery (D'Angiulli et al., 2013b). We hypothesized that high-vividness items, compared to low-vividness ones, would show one of the following patterns at retrieval: (1) an earlier time course of alpha desynchronization, reflecting a more rapid access to the encoded mnemonic information, (2) an increase in alpha desynchronization, reflected by a greater decrease in alpha power, which would suggest the retrieval of more or stronger mnemonic information for high vivid items, or (3) both an earlier and greater increase in desynchronization for items encoded as high in vividness.

3.2 Methods

3.2.1 Participants

Thirty-one participants between the ages of 18 and 35 (*M* = 23.0, *SD* = 3.39) were recruited through Duke University's Psychology Subject Pool and Interdisciplinary Behavioral Research Center. Participants provided informed consent and were either credited (1 per hour) or paid ($15 per hour) for their time, in accordance with a protocol approved by the Duke University Medical Center Institutional Review Board. Participants were all right-handed and had normal or corrected-to-normal vision with no history of neurological or psychiatric diseases. The study took approximately 90 min to complete and was preceded by a 1 hr setup.

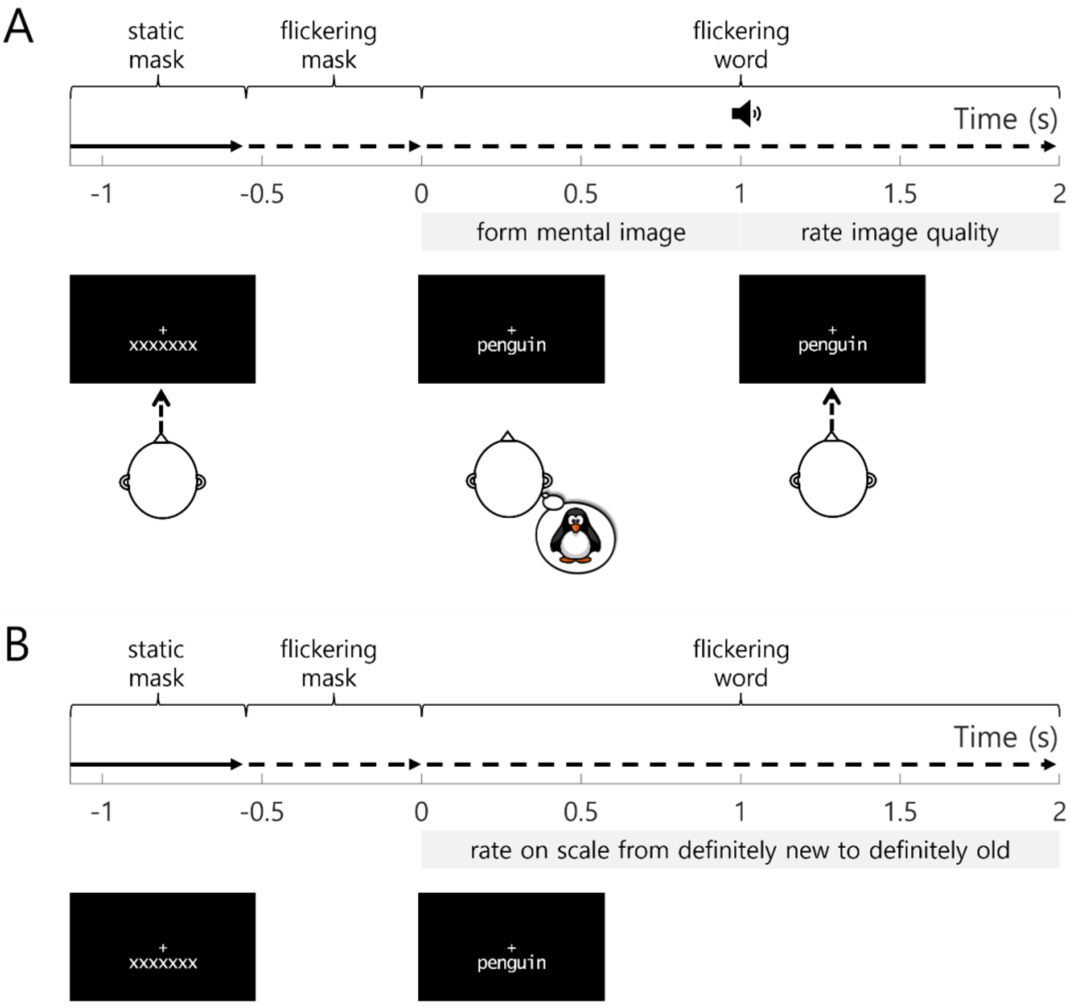

Figure 6: Task paradigm. Participants were first presented with a mask stimulus, which was static for the first half of its presentation and flickering at 18 Hz for the second half. The mask stimulus was then immediately followed by a flickering object-word stimulus that was presented for 2 s. A) During the encoding phase, participants were instructed to form a visual mental image for each word. After 1 second, they heard a tone indicating that they should rate the quality of the image they formed on a scale of 1 (poor/no image) to 4 (excellent). B) During the retrieval phase, participants were instructed to identify the word as old or new and rate their confidence from 1 (definitely new) to 6 (definitely old). They had the full 2 s to make their response.

3.2.2 Stimuli and procedure

Participants were seated 80 cm from a 24-inch stimulus presentation monitor (144 Hz refresh rate) in a dimly lit, electrically shielded room. The study consisted of an encoding phase (600 trials) and retrieval phase (900 trials), separated by a 5-min break. For both phases, participants maintained fixation on a white cross in the middle of a black screen. Stimulus presentation was controlled using Presentation 20.1 Software (Neurobehavioral Systems, Inc., Berkeley, CA). At the start of each trial, a static mask stimulus was presented just below the fixation cross for 555.6 ms. The mask consisted of a row of 5-7 lowercase Xs. After 555.6 ms, the mask began to flicker at 18 Hz for another 555.6 ms and was then replaced by a flickering 5-7 letter object word or non-word stimulus for 2 s. Object word stimuli appeared on 95% of trials and non-word stimuli on the remaining 5%. For consistency in visual input, the mask, word, and non-word stimuli were presented using a monospaced font (Lucida Console, size 24) and grouped so that all 5-letter stimuli appeared in a row, followed by the 6- and then 7-letter stimuli. There were an equal number of 5-, 6-, and 7- letter words.

During the encoding phase, participants were instructed to form a mental image of each object-word stimulus, with as much imagery detail as possible, for the first 1 s of the stimulus presentation. After 1 s, a tone was presented and participants had the remaining 1 s to rate the image vividness on a scale of 1 (poor/no image) to 4 (excellent image). Responses were made on a keyboard using their left hand. During the non-word stimulus trials, participants were instructed to just press the space bar with their left-hand thumb as quickly as possible. The non-word stimulus trials were included to encourage participants to maintain vigilant attention during the mask presentation because they required an immediate response after the offset of the mask stimulus. The encoding phase took ~ 35 min to complete and consisted of 5 blocks (120 trials per block), with breaks in between each block.

The retrieval phase was a surprise to participants to ensure that encoding would be incidental. All 570 object-word stimuli from encoding were presented with an additional 285 new words and 45 new non-words. The trials were presented with the same procedure as the encoding phase, with the mask stimulus followed by either a word (95% of trials) or non-word stimulus. Again, the mask was presented static for the first 555.6 ms and flickering for another 555.6 ms. Similarly, the word and non-word stimuli were presented flickering at 18 Hz for 2 s. However, in contrast to the encoding phase, there was no tone presented at any point during the retrieval phase. Participants were tasked with determining whether each word was old or new and rating their confidence on that from 1 (definitely new) to 6 (definitely old). On the non-word stimulus trials, participants again were instructed to respond by pressing the space bar as quickly as possible. The retrieval phase took ~ 50 min to complete and consisted of 5 blocks (180 trials per block), with breaks in between each block.

3.2.3 Behavioral data and analysis

Trials were excluded if participants responded within 150 ms of the onset of the word stimulus or if they failed to make a response. To evaluate general retrieval performance, participants' accuracy data were submitted to a one-way (confidence: low/medium/high) repeated-measures analysis of variance (rANOVA). Additionally, participants' reaction time data at retrieval were submitted to a 2 (memory: remembered/forgotten) × 3 (confidence: low/medium/high) rANOVA. As in our previous paper (Gjorgieva et al., 2022) that investigated the encoding of visual mental images, the vividness levels were established by binning trials into a High Vividness (*HighViv*) level and a Low Vividness (*LowViv*) level. The HighViv level included retrieval trials for items that had been rated at the highest vividness rating (4) at encoding, and the LowViv level included retrieval trials for items that had been rated at the two lowest vividness ratings (1 and 2) at encoding, which enabled trial counts for the two conditions to be relatively similar. HighViv and LowViv items were compared in terms of their reaction times (RTs) and confidence ratings at retrieval using paired-sample t-tests. For a more direct comparison of vividness, we also controlled for both memory accuracy and confidence by comparing RTs for high- and low-vividness items that were all successfully remembered with high-confidence (*HighViv-RemHighConf* and *LowViv-RemHighConf)*.

3.2.4 EEG data acquisition and preprocessing

Online EEG data were recorded for both phases, and the data from the encoding phase have been previously reported (Gjorgieva et al., 2022). A custom, 64-channel, extended-coverage cap (Woldorff et al., 2002) was used with active electrodes (actiCAP, Brain Products GmbH) and an online right-mastoid reference. Impedences were maintained below 5 kOhms for the ground and mastoid electrodes and below 15 kOhms for the remaining electrodes. Data were digitized at 500 Hz per channel, with a three-stage cascaded integrator low-pass comb filter with a 130 Hz corner frequency. One electrode was positioned below the left eye for the vertical electrooculogram (EOG), and two electrodes were positioned lateral to the outer canthus of each eye for the horizontal EOG channel. These electrodes were used to monitor for blinks and horizontal eye movements.

Offline, the data were first filtered with a 40 Hz low-pass filter, then downsampled to 250 Hz, then filtered with a 0.1 Hz high-pass causal FIR filter, and finally re-referenced to the algebraic average of the left and right mastoid electrodes. Excessively noisy channels were interpolated using a spherical spline procedure (Perrin et al., 1989). The data were epoched from -2750 to 3750 ms, relative to the onset of the word or non-word stimuli. Eyeblinks that occurred near stimulus onset and could subsequently influence the initiation of the neural processing cascade were detected by submitting the data to an algorithm using a 150-ms wide window moving in 50-ms steps from -100 to 300 ms. Any epochs with peak-to-peak voltage differences that exceeded 40 μV in the vertical EOG channel were marked for rejection. We conducted an infomax independent component (IC) analysis on a copy of the EEG data that was epoched from -1100 to 200 ms to avoid overlapping trials. The resulting component weights were transferred back to the original data set and ocular components reflecting eyeblinks were removed from the data (at most 4 per participant). Horizontal eye movements were detected by submitting data to an algorithm using a 150-ms moving window. The window moved across the epoch from -100 to 2000 ms in 50-ms steps and marked for rejection the epochs with peak-to-peak voltage differences that exceeded 24 μV (corresponding to approximately 1.5° of eye movement) in the vertical EOG channel. The final data-cleaning procedure removed any high-amplitude noise or excess muscle activity. For this procedure, when three or fewer electrodes (excluding the vertical and horizontal EOG channels) exceeded ±100 μV for an epoch, each of these electrodes were replaced using the spherical-spline interpolation procedure. Alternatively, when more than three electrodes exceeded the threshold, the epoch was marked for rejection

Eight participants were excluded due to >70% of trials being rejected, either due to poor EEG data quality (n = 5), or a combination of both (n = 3). This left 23 participants in the final analyses (15 female, mean age 22.5 years). The nonword-stimulus catch trials were also excluded from the final analyses. Data were preprocessed and analyzed in MATLAB with a combination of EEGLAB , ERPLAB (Lopez-Calderon & Luck, 2014), and FieldTrip (Oostenveld et al., 2011). The EEG cap featured a custom-modified 10-10, equidistant electrode montage with extended inferior occipital coverage (Woldorff et al., 2002). Electrode sites in our montage are reported based on standard 10-10 electrode names for electrodes within 5 mm of the corresponding 10-10 site. If the electrodes were 5-10 mm from the 10-10 site, the name has a prime appended to it. If the electrodes were 10-15 mm from the 10-10 site, a subscript ‘a’ was added for electrodes anterior to the listed 10-10 site, and a ‘p’ was added for those posterior to the 10-10 site. No electrodes were further than ~15 mm from their closest standard 10-10 site.

3.2.5 EEG and ERP analysis

For the ERP analysis, we examined the parietal old/new effect by selectively averaging trials that were time-locked to the onset of the word stimuli during the retrieval phase. Based on previous literature (Friedman & Johnson, 2000; Woodruff et al., 2006; Wynn et al., 2019), we selected a cluster of electrodes that centered on Pz and included electrodes P1′ and P2′. To investigate the effect of memory, we compared retrieval trials of old items that were successfully remembered (*Rem)* to retrieval trials of new items that were correctly identified as new (*CorrRej*). Trials in which participants rated their confidence at the lowest level were excluded, as their accuracy rate was near chance (M = 56.8%). Mean amplitude data were submitted to a 2 (memory: Rem/CorrRej) × 4 (time: 400-500/500-600/600-700/700-800) rANOVA in 100 ms time bins, and post-hoc paired sample t-tests were conducted to identify any significant differences between the two conditions within each time bin. Similarly, to evaluate the effect of vividness (while controlling for memory and confidence), we focused only on retrieval trials for old items that were successfully remembered with high-confidence and subdivided them based on whether the items had been rated as high-vividness (*HighViv-RemHighConf*) or low-vividness (*LowViv-RemHighConf*) at encoding. Mean amplitude data were submitted to a 2 (vividness: HighViv-RemHighConf/LowViv-RemHighConf) × 4 (time: 400-500/500-600/600-700/700-800) rANOVA in 100 ms time bins. Post-hoc paired sample t-tests were again conducted to identify significant differences between conditions within each time bin.

To ensure that the ERP results were distinct from the oscillatory results, the average ERP of each condition was subtracted out from the raw waveform on each trial that was in that condition. Then, frequency decomposition of the EEG was performed using multitaper methods that were based on discrete prolate spheroidal sequences to estimate power in logarithmically spaced frequencies ranging from 3 to 40 Hz. The taper window widths were 3 cycles for 3 Hz, 4 cycles for 4-7 Hz, 5 cycles for 8-14 Hz, 7 cycles for 15-20 Hz, and 10 cycles for 21-40 Hz. Spectral smoothing through multitapers was calculated as $5 \times \log_{10}$ of each frequency. We performed a decibel conversion to normalize and baseline the data relative to the static presentation of the mask stimulus (-848 to -600 ms relative to the onset of the word stimulus).

As noted above, the focus here was on the power changes in the alpha band (8-12 Hz). In particular, posterior alpha power was calculated as the average oscillatory activity between 8 and 12 Hz across a cluster of electrodes centered on electrodes Pz and pOz, and including electrodes O1’, O2’, PO1, PO1, PO5, PO6, P3a, P4a, C5p, and C6p. To evaluate the effect of memory on alpha power, mean alpha-power data were submitted to a 2 (memory: Rem/CorrRej) × 6 (time: 500-600/600-700/700-800/800-900/900-1000/1000-1100) rANOVA in 100 ms time bins. Post-hoc paired sample t-tests were conducted to identify time bins that were significantly different between conditions. To evaluate the effect of vividness, mean alpha power data were submitted to a 2 (vividness: HighViv-RemHighConf/LowViv-RemHighConf × 6 (time: 500-600/600-700/700-800/800-900/900-1000/1000-1100) rANOVA in 100 ms time bins. Again, post-hoc paired sample t-tests were conducted to identify time bins that differed significantly between conditions.

In addition to the amplitude analyses, we conducted latency analyses on alpha. The time-point for the peak latency was identified for each condition of interest on every subject searching from 0 to 1500 ms. We conducted paired sample t-tests to compare Rem and CorrRej trials at retrieval, as well as HighViv-RemHighConf and LowViv-RemHighConf trials.

3.3 Results

3.3.1 Behavioral results

We evaluated retrieval performance as measured by accuracy for correctly identifying old and new items. Participants correctly identified 83.6% of old items as old (SD = 10.8) and 71.7% of new items as new (SD = 13.0). Furthermore, participants were more accurate at correctly identifying the old items that had been encoded with high-vividness (M = 89.1, SD = 6.9) compared to low-vividness (M = 78.6, SD = 15.1), t(22) = 4.38, p < .001, d = .91. We also compared accuracy for identifying old and new items based on the self-reported confidence levels. Data were submitted to a one-way ANOVA with three levels (confidence: low/medium/high), which showed a significant effect of confidence, F(2, 40) = 76.15, $p < .001$, $n_p^2 = .79$. We observed improved accuracy for higher-confidence items (low: $M = 56.8$, $SD = .06$, medium: $M = 73.8$, $SD = .14$, high: $M = 87.1$, $SD = .09$). Post-hoc paired sample t-tests showed that accuracy was significantly higher for the high confidence compared to medium confidence items, $t(20) = -4.69$, $p < .001$, d = -1.02, as well as for the medium confidence compared to low confidence items, $t(20) = -6.35$, $p < .001$, d = -1.39. This analysis confirmed that the confidence levels were indicative of stronger memory. The trials with the lowest confidence level were excluded from subsequent analyses because their accuracy was near chance.

We assessed RTs at retrieval by comparing the levels of confidence (low, medium, and high) for remembered and forgotten items. The RT data were submitted to a 2 (memory: remembered/forgotten) × 3 (confidence: low/medium/high) rANOVA (**Fig 7**). Results showed a significant effect of memory, F(1, 16) = 18.96, $p < .001$, $n_p^2 = .54$, indicating differences in RTs for remembered vs. forgotten items. Additionally, there was a main effect of confidence, F(2, 32) = 4.79, $p = .02$, $n_p^2 = .23$, indicating a difference in RTs based on the self-reported level of confidence at retrieval. Most critically, there was an interaction between memory and confidence, F(2, 32) = 15.41, $p < .001$, $n_p^2 = .49$. Post-hoc paired sample t-tests showed that this interaction was driven by a significant difference in RTs between high-confidence remembered items ($M = 1029$, $SD = 100$) and the rest of the conditions. More specifically, RTs were significantly faster for high-confidence remembered items than those remembered with medium-confidence (*M* = 1267 *SD* = 170; *t*(15) = 4.32, *p* < .001) and low-confidence (*M* = 1276, *SD* = 191; *t*(15) = 4.65, *p* < .001). Additionally, the items remembered with high-confidence had significantly faster RTs compared to items forgotten with high-confidence (*M* = 1252, *SD* = 171; *t*(15) = 6.93, *p* < .001), medium-confidence (*M* = 1295, *SD* = 231; *t*(15) = 5.29, *p* < .001), and low-confidence (*M* = 1283, *SD* = 214; *t*(15) = 4.69, *p* < .001). Taken together, the RT and accuracy results suggest that the high-confidence remembered items were remembered with the greatest fidelity and speed compared to the other categories. This is in line with prior research suggesting that items remembered with high confidence are more reflective of recollection, while items remembered with lower confidence are more reflective of familiarity (Curran, 2004; Düzel et al., 1997; Wilding & Rugg, 1996; Wynn et al., 2019; Yonelinas, 2001, 2002).

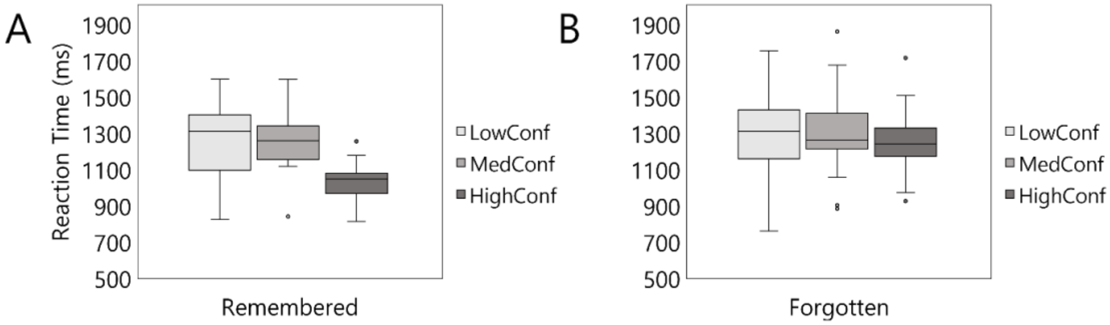

Figure 7: Reaction times for memory retrieval. The left panel shows the mean and distribution of RTs for the successfully remembered old items split based on self-reported confidence levels. The right panel shows the mean and distribution of RTs for the forgotten old items divided by confidence level. Participants were fastest at

making a response for items they remembered with high confidence. There was a significant difference (*p* < .001) between the items remembered with high confidence and all other categories. There were no significant differences amongst the other categories.

Once we had a better understanding of the memory retrieval overall, we examined differences in memory retrieval for items that had been rated as high- vs. low-vividness (HighViv and LowViv) at encoding by comparing RTs and confidence ratings for the two categories. We observed faster RTs at retrieval for the HighViv (*M* = 1039, *SD* = 115) compared to LowViv items (*M* = 1113, *SD* = 135), *t*(22) = -8.16, *p* < .001, d = -1.70 (**Fig 8A**). The confidence ratings ranged from 1 (definitely new) to 6 (definitely old). A '1' rating for an old item would indicate that the participant incorrectly identified the old item as new and were highly-confident, while a '6' rating would indicate that the participant correctly identified the old item as old with high confidence. Participants reported higher confidence ratings for the HighViv (*M* = 5.40, *SD* = .35) over LowViv items (*M* = 4.91, *SD* = .60), *t*(22) = 5.27, *p* < .001, d = 1.10 (**Fig 8B**). We then controlled for confidence by comparing the effects of vividness at encoding only for the items remembered with high confidence (HighViv-RemHighConf vs. LowViv-RemHighConf). Again, results showed faster RTs for the HighViv-RemHighConf items (*M* = 996, *SD* = 96) compared to LowViv-RemHighConf (*M* = 1071, *SD* = 98), *t*(22) = -11.86, *p* < .001, d = -2.47 (**Fig 8C**). This finding confirmed that the vividness-related RT difference was not accounted for just by differences in confidence.

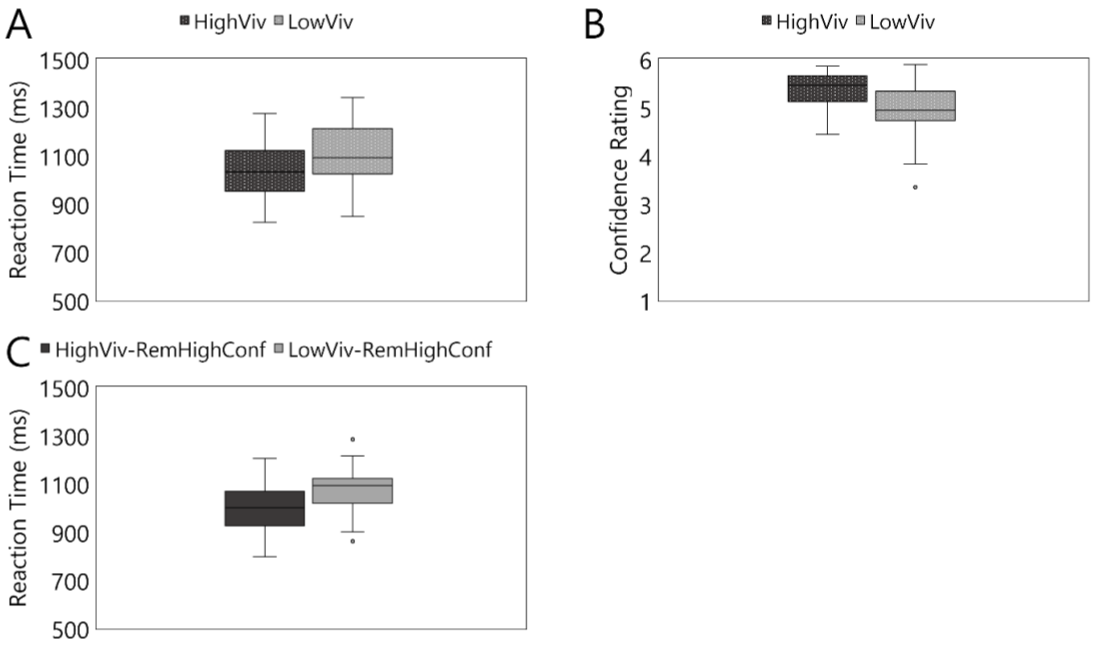

Figure 8: Reaction times and confidence ratings for the high-vividness compared to low-vividness items. A) The mean and distribution of RTs at retrieval for items that had been rated as high- and low-vividness at encoding. Participants were faster at rating their confidence in their response for the high-vividness items. B) The mean and distribution for confidence levels at retrieval ranging from 1 (definitely new) to 6 (definitely old). Participants were more confident when identifying items that had been rated as high-vividness at encoding. C) The mean and distribution of RTs at retrieval for the items successfully remembered with high confidence as a function of image vividness at encoding. Controlling for both memory and confidence, we observed faster RTs for the high-vividness items that had been successfully remembered with high-confidence compared to the low-vividness items that had also been successfully remembered with high-confidence.

3.3.2 ERP results

For the EEG analysis, our first goal was to examine episodic memory retrieval via the parietal old/new ERP effect. Based on prior research finding a modulation of the parietal old/new effect due to memory (Rugg & Curran, 2007), we expected an increase in magnitude for the remembered old items compared to the new items that were correctly identified as new. To examine these differences based on memory, ERP data were submitted to a 2 (memory: Rem/CorrRej) × 4 rANOVA (time: 400-500ms/500-600ms/600-700ms/700-800ms). The results indicated a main effect of memory, F(1, 22) = 9.17, $p = .006$, $n_p^2 = .29$, and a significant main effect of time, F(3, 66) = 11.58, $p < .001$, $n_p^2 = .35$. Additionally, there was a significant interaction between these two factors, F(3, 66) = 5.81, $p = .001$, $n_p^2 = .21$. **Figure 11A** displays the mean amplitude and within-subject standard error for each time bin. Post-hoc paired sample t-tests showed an increased magnitude (larger positivity) for the successfully remembered items compared to the correctly identified new items between 400 and 700 ms (**Fig 9**). **Table 4** displays the means and standard deviations for each condition, as well as the results of the post-hoc t-tests for each time bin.

Table 4: Post-hoc paired sample t-tests comparing Rem and CorrRej ERP activity across time.

	Rem Mean (SD)	CorrRej Mean (SD)	t	df	p	d
400 – 500 ms	2.41 µV (3.92)	1.18 µV (4.53)	3.59	22	.002*	.75
500 – 600 ms	4.38 µV (4.66)	2.85 µV (4.46)	3.88	22	<.001*	.81
600 – 700 ms	5.70 µV (4.44)	4.08 µV (4.33)	3.25	22	.004*	.68
700 – 800 ms	4.78 µV (3.95)	4.46 µV (3.96)	.63	22	.539	.13

*Note: * indicates p<.05*

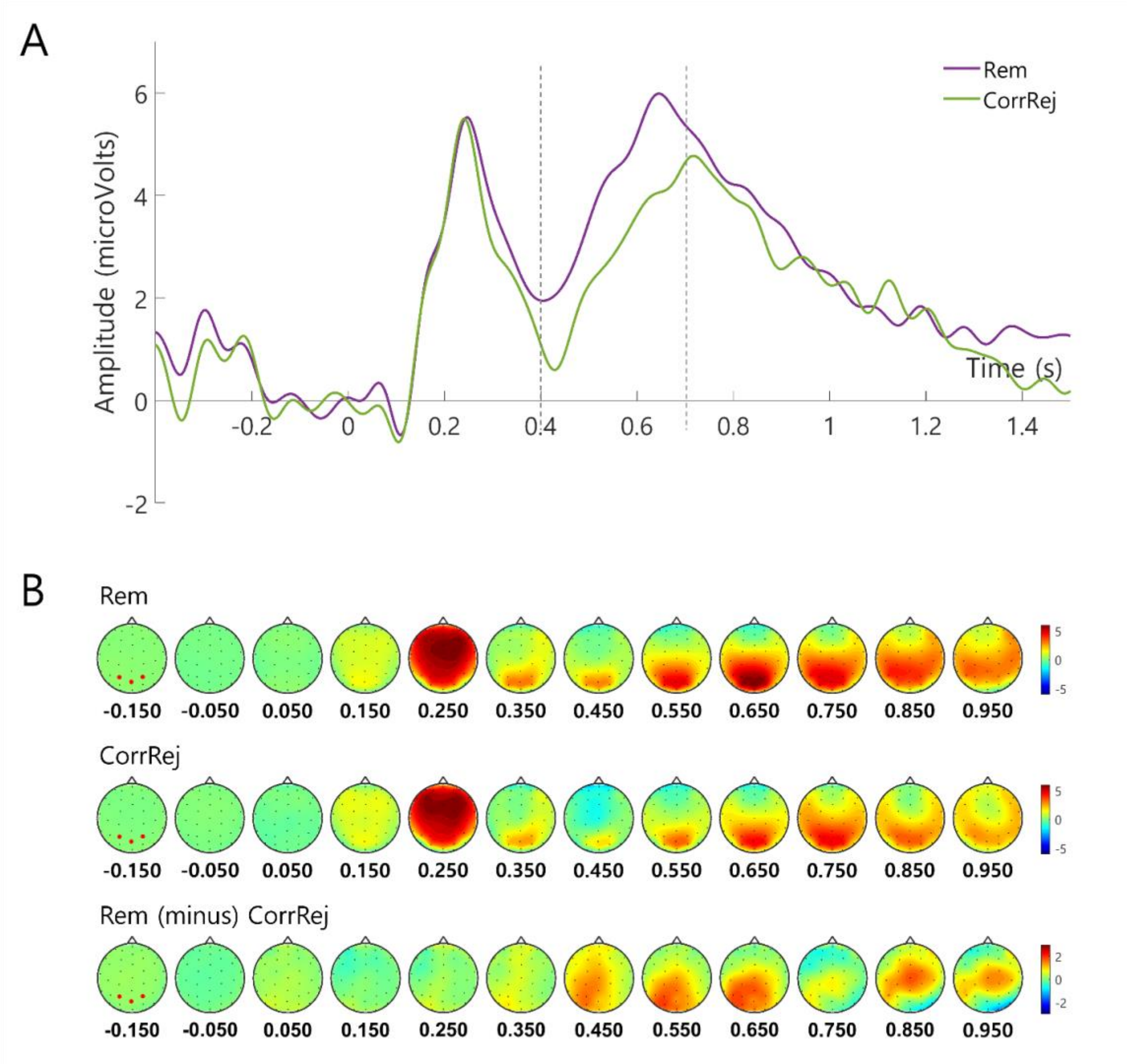

Figure 9: Effect of memory on the parietal old/new ERP effect. A) Timelock-averaged data relative to the onset of the word stimulus during a retrieval trial. Results showed significant differences ($p < .05$) between the items successfully remembered and items successfully identified as new between 400 and 700 ms (indicated by the vertical dashed lines), with an increased magnitude for the remembered items. B) The topographic plots show the trial time-course of each condition in 100 ms time bins. Each bin is labeled with the middle time point of the 100 ms period.

More critical to our research question, we wanted to examine differences based on vividness in the parietal old/new effect while controlling for memory accuracy and confidence. We hypothesized that if the high-vividness items were recalled with greater fidelity, we would observe an increased magnitude in the parietal old/new effect in comparison with the low-vividness items. We calculated the difference waves for the HighViv-RemHighConf and LowViv-RemHighConf items relative the correctly rejected new items by subtracting the CorrRej ERP from both HighViv-RemHighConf and LowViv-RemHighConf. The difference wave data were submitted to a 2 (memory: HighViv-RemHighConf/ LowViv-RemHighConf) × 4 (time: 400-500ms/500-600ms/600-700ms/700-800ms) rANOVA. Unlike the comparison based on memory, the results of this analysis showed no main effect of vividness on this ERP effect, $F(1, 22) = 1.13$, $p = .299$, $n_p^2 = .05$. We did observe a main effect of time, $F(3, 66) = 4.83$, $p = .004$, $n_p^2 = .18$, but importantly, there was no interaction, $F(3, 66) = 1.42$, $p = .245$, $n_p^2 = .06$. There were no differences in the parietal old-new ERP effect when comparing high- and low-vividness items that had been remembered with high confidence (**Fig 10**). **Table 5** displays the means and standard deviations for each condition, and **Figure 11B** displays the mean amplitude and within-subject standard error for each time bin. Our findings suggest that high- and low-vividness items were retrieved fairly equivalently, at least as reflected by the parietal old/new effect.

Table 5: Mean and standard deviations of HighViv-RemHighConf [MINUS] CorrRej and LowViv-RemHighConf [MINUS] CorrRej difference waves across time.

	HighViv-RemHighConf [MINUS] CorrRej	LowViv-RemHighConf [MINUS] CorrRej

	Mean (SD)	Mean (SD)
400 – 500 ms	1.30 μV (.44)	.95 μV (.40)
500 – 600 ms	1.77 μV (.50)	1.18 μV (.53)
600 – 700 ms	2.06 μV (.68)	1.40 μV (.60)
700 – 800 ms	.49 μV (.64)	.47 μV (.52)

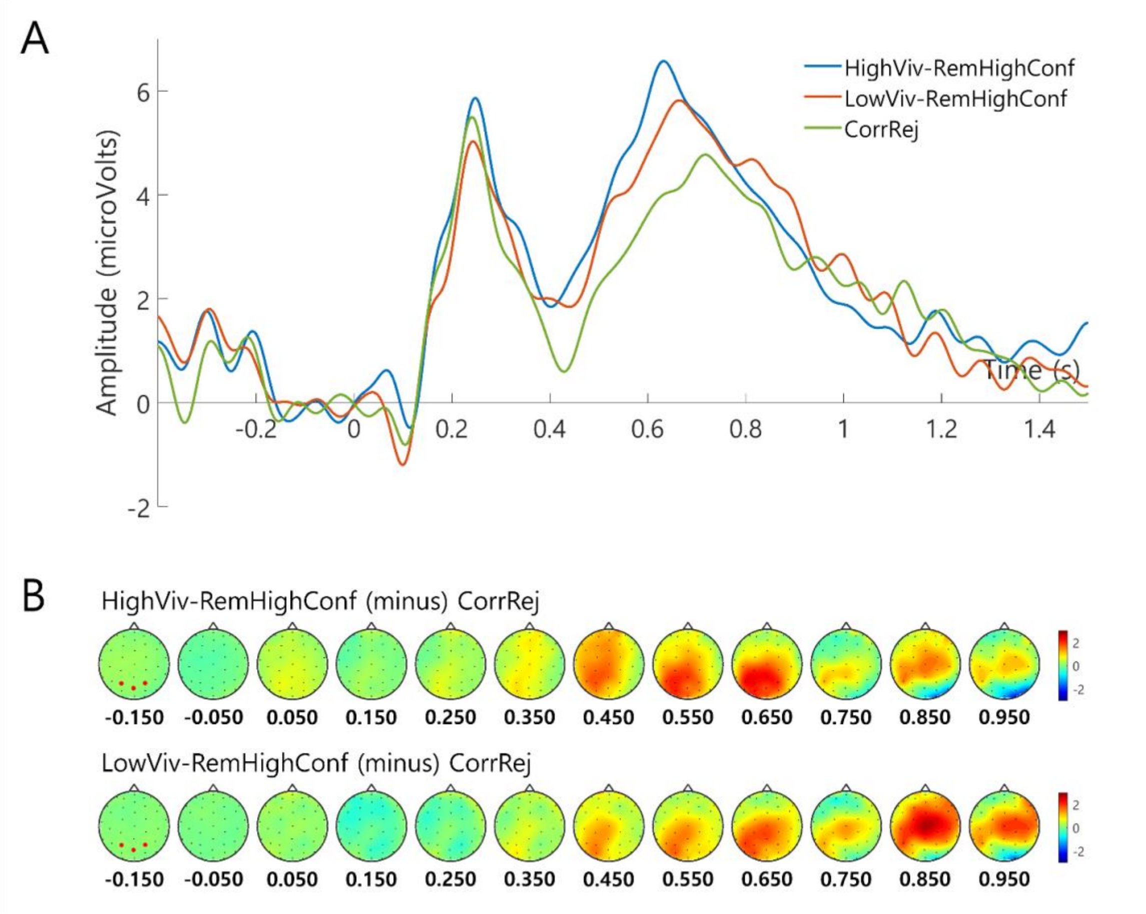

Figure 10: Effect of vividness on the parietal old/new ERP effect. A) Timelock-averaged data comparing the effect of the vividness rating at encoding during memory retrieval for items remembered with high confidence. Findings showed no significant differences on this retrieval ERP effect for items that had been encoded with high-vividness compared to those that had been encoded with low-vividness. B) The topographic plots show the time-course for each condition in 100 ms time bins, each labeled with the middle time point of the period.

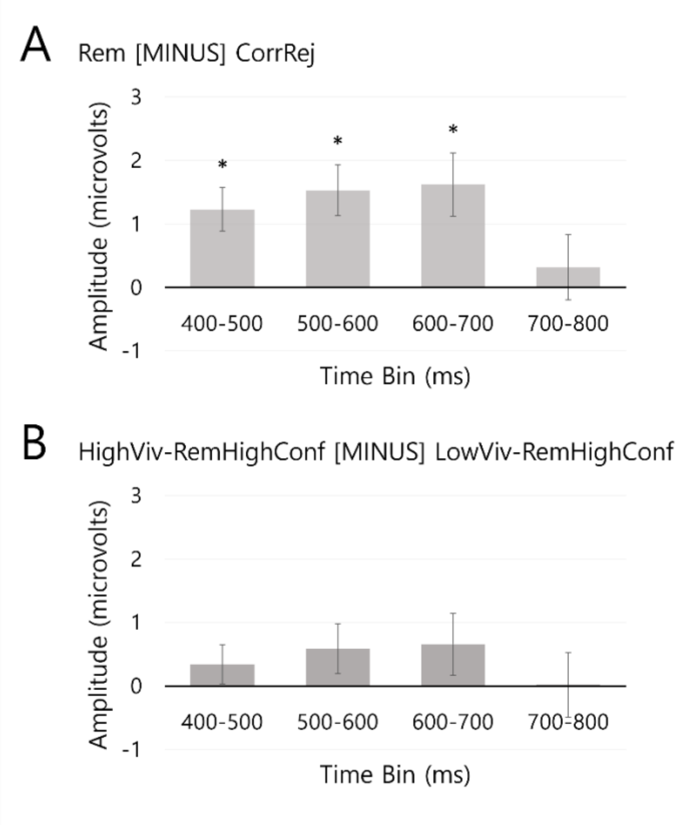

Figure 11: Within-subject differences for the parietal old/new effect. A) The Rem minus CorrRej calculation for the parietal old/new effect within each time bin with error bars indicating the within-subject standard error. The asterisk indicates $p <$ .05. B) The difference between HighViv-RemHighConf and LowViv-RemHighConf was calculated for the parietal old/new ERP within each time bin. Error bars indicate the within-subject standard error. There were no significant differences between the conditions in this ERP activity.

3.3.3 Oscillatory results

Based on previous research identifying parietal alpha as an index of memory strength at retrieval (Griffiths et al., 2019; Martín-Buro et al., 2020), we evaluated the effects of memory and vividness at retrieval. We hypothesized that the effect of memory would be reflected by a difference in amplitude of the parietal alpha power. Specifically, we predicted that the decrease in alpha power would be greater for old items that were successfully remembered compared to new items correctly identified as new, also referred to as correct rejections. Data were submitted to a 2 (memory: Rem/CorrRej) × 6 (time: 500-600ms/600-700ms/700-800ms/800-900ms/900-1000ms/1000-1100ms) rANOVA. **Figure 12A** displays the time-course and **Figure 12B** the topography of alpha power at retrieval for the Rem and CorrRej items. Results showed no main effect of memory, *F*(1, 22) = 1.52, *p* = .230, n_p^2 = .07, and no main effect of time, *F*(5, 110) = 1.35, *p* = .249, n_p^2 = .06. Critically, we observed a significant interaction of these two factors, *F*(5, 110) = 3.54, *p* = .005, n_p^2 = .14. **Figure 14A** displays the mean amplitude and within-subject standard error for each time bin. Post-hoc paired sample t-tests conducted at each time bin revealed significant differences between the Rem and CorrRej items from 800 to 900 ms, as well as a trending difference from 700 to 800 ms. **Table 6** displays the means and standard deviations for each condition and the t-test results at each time bin. In line with previous studies (Griffiths et al., 2019; Martín-Buro et al., 2020), these results suggest that memory at retrieval is reflected by alpha power, with a larger decrease indicating stronger memory, beginning weakly at 700 ms after the onset of the word stimulus, with a robust difference starting at 800 ms.

Table 6: Post-hoc paired sample t-tests comparing Rem and CorrRej alpha power across time.

	Rem Mean (SD)	CorrRej Mean (SD)	t	df	p	d
500 – 600 ms	-2.55 dB (1.25)	-2.65 dB (1.21)	.85	22	.406	.18
600 – 700 ms	-2.83 dB (1.30)	-2.70 dB (1.19)	-.94	22	.358	-.20
700 – 800 ms	-2.98 dB (1.27)	-2.67 dB (1.31)	-1.79	22	.087**	-.37

800 – 900 ms	-2.93 dB (1.25)	-2.56 dB (1.28)	-2.12	22	.045*	-.44
900 – 1000 ms	-2.71 dB (1.30)	-2.44 dB (1.26)	-1.46	22	.158	-.30
1000 – 1100 ms	-2.37 dB (1.34)	-2.25 dB (1.42)	-.57	22	.572	-.12

*Note: * indicates p<.05 and ** indicates p<.10*

In addition to the amplitude analysis, we performed a peak latency analysis for the alpha power dip. For each subject, we identified the peak alpha time-point between 0 and 1500 ms for the two conditions (Rem and CorrRej). These data were submitted to a paired sample t-test, which showed no significant difference between the Rem items (*M* = 723, *SD* = 188) and CorrRej items (*M* = 809, *SD* = 371) items, *t*(22) = -1.24, *p* = .228, d = -.26. Thus, the time-course of the alpha dip was similar between these two conditions.

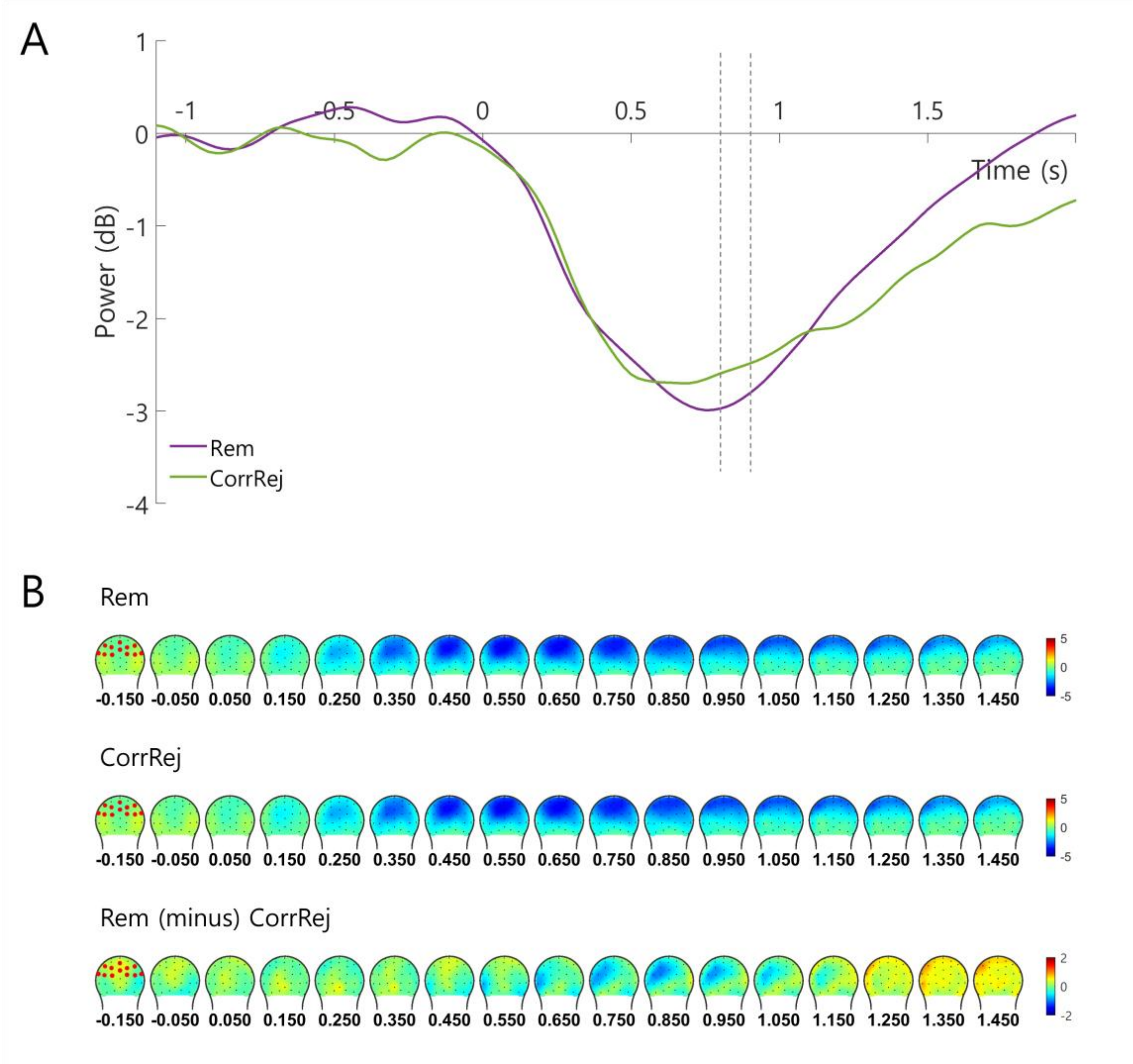

Figure 12: Effect of memory on alpha power. A) Timelock-averaged parietal alpha power plotted over the time-course of a retrieval trial. Time 0 indicates the onset of the word stimulus. Results showed significant differences (p < .05) between the remembered items and items successfully identified as new between 800 and 900 ms (indicated by the dashed lines), as well as a trending difference (p < .10) between 700 and 800 ms. Remembered items showed decreased alpha power compared to the correctly identified as new items. However, there were no differences in the latency of the alpha effect. B) The topographic plots show the time-course of the trial for each condition in 100 ms time bins. Each bin is labeled with the middle time point for each 100 ms period.

To evaluate the effects of vividness, we conducted the same set of analyses to compare the HighViv-RemHighConf and LowViv-RemHighConf items. For the amplitude analysis, data were submitted to a 2 (vividness: HighViv-RemHighConf/LowViv-RemHighConf) × 6 (time: 500-600ms/600-700ms/700-800ms/800-900ms/900-1000ms/1000-1100ms) rANOVA. **Figure 13A** displays the time-course and **Figure 13B** the topography of alpha power at retrieval for the HighViv-RemHighConf and LowViv-RemHighConf items. Our results showed no main effect of vividness across the total analyzed time period, $F(1, 22) = .29$, $p = .597$, $n_p^2 = .01$, and a weak trending main effect of time, $F(5, 110) = 1.86$, $p = .108$, $n_p^2 = .08$. However, we observed a significant interaction of these two factors, $F(5, 110) = 11.44$, $p < .001$, $n_p^2 = .34$, indicating that the effects on the magnitude differed at distinct time points for high-vividness versus low-vividness items. **Figure 14B** displays the mean amplitude and within-subject standard error for each time bin. Post-hoc paired sample t-tests comparing the low- and high-vividness items showed a significant difference between 900 and 1100 ms, with decreased alpha power for the low-vividness items during these periods. Additionally, there was a trending difference following the same patten from 800 to 900 ms. **Table 7** displays the means and standard deviations for each condition and the t-test results at each time bin. Importantly, it can be seen that these significant differences in alpha power were accompanied by an apparent difference in latency, with an earlier latency of the decrease in alpha power for the high-vividness items. Accordingly, we conducted an analysis on the latency of alpha as well.

Table 7: Post-hoc paired sample t-tests comparing HighViv-RemHighConf and LowViv-RemHighConf alpha power across time.

	HighViv-RemHighConf Mean (SD)	HighViv-RemHighConf Mean (SD)	t	df	p	d
500 – 600 ms	-2.85 dB (1.44)	-2.53 dB (1.35)	-1.12	22	.276	-.23
600 – 700 ms	-3.25 dB (1.57)	-2.73 dB (1.43)	-1.73	22	.098	-.36
700 – 800 ms	-3.27 dB (1.47)	-3.06 dB (1.38)	-.81	22	.426	-.17
800 – 900 ms	-2.93 dB (1.42)	-3.29 dB (1.24)	1.85	22	.077**	.39
900 – 1000 ms	-2.56 dB (1.56)	-3.19 dB (1.29)	2.99	22	.007*	.62
1000 – 1100 ms	-2.15 dB (1.54)	-2.87 dB (1.43)	2.99	22	.007*	.62

*Note: * indicates p<.05 and ** indicates p<.10*

For the peak latency analysis, we hypothesized that the HighViv-RemHighConf items would have a faster latency alpha effect at retrieval, in line with the theory suggesting faster access to sensory memory traces for high-vividness items (D'Angiulli et al., 2013b). We compared the peak amplitude latencies for the HighViv-RemHighConf and LowViv-RemHighConf items using a paired sample t-test. In line with our hypothesis, we observed a faster latency of the negative peak of the alpha power time course for the high-vividness (*M* = 683, *SD* = 200) compared to low-vividness (*M* = 821, *SD* = 201) items, *t*(22) = -3.05, *p* = .006, d = -.64. These neural findings suggest that the high-vividness items were retrieved more quickly than the low-vividness items, consistent with the faster RTs that followed. This faster retrieval of the high-vividness items then ramifies into the difference in amplitude that we observed afterwards. More specifically, the retrieval process begins and concludes more quickly for the high-vividness items than for the low-vividness, even though they all are remembered with high confidence.

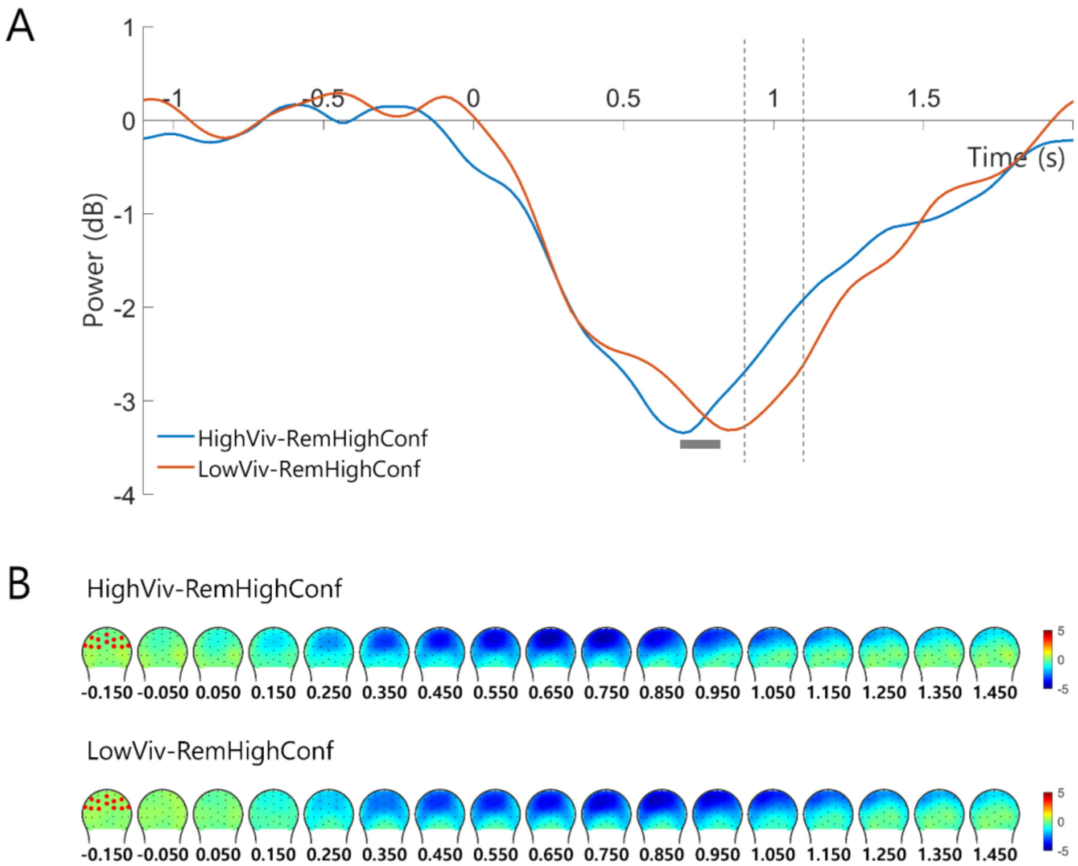

Figure 13: Effect of vividness on alpha power when controlling for confidence. A) Timelock-averaged parietal alpha power plotted over the time-course of a retrieval trial, with the onset of the word stimulus occurring at time 0. Results showed a significant difference (*p* < .05) between 900 and 1100 ms (indicated by the vertical dashed lines), as well as a trending difference (*p* < .10) from 800 to 900 ms. Moreover, we observed a significant difference in the latency of the alpha effect, whereby the high-vividness items remembered with high confidence were represented by a faster decrease in alpha power compared to the low-vividness items remembered with high confidence. B) The topographic plots show the time-course of the trial for each condition in 100 ms time bins. Each bin is labeled with the middle time point for each 100 ms period.

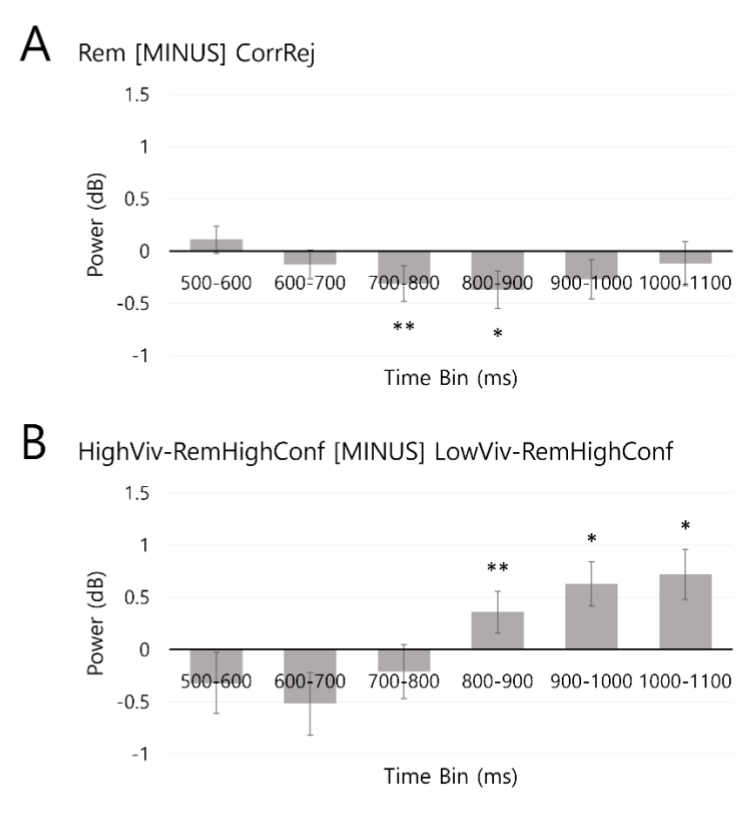

Figure 14: Within-subject differences for alpha. A) The difference between Rem and CorrRej was calculated for alpha power within each time bin, with error bars indicating the within-subject standard error. One asterisk indicates $p < .05$ and two asterisks indicate $p < .10$. B) The HighViv-RemHighConf minus LowViv-RemHighConf difference within each time bin for the alpha power. Error bars indicate the within-subject standard error, with one asterisk indicating $p < .05$ and two asterisks indicating $p < .10$.

3.4 Discussion

In this study, subjects were asked to generate visual mental images of a series of object words and rate the vividness of those images. After the generation of this series of mental images, subjects completed a surprise old/new recognition task, which included rating their memory confidence. Using this paradigm, we replicated the alpha power decrease for successfully remembered items (Martín-Buro et al., 2020) and the decreased reaction time for high-vivid encoded items (D’Angiulli et al., 2013b). We also provided new neural evidence indicating that items that were imaged with high-vividness at encoding produce an earlier decrease in alpha band activity at retrieval compared to low-vividness ones. This result links previous behavioral research about mental imagery (D’Angiulli et al., 2013b; Yi et al., 2008) with neural research about alpha band desynchronization and memory-retrieval processes (Koenig-Robert & Pearson, 2019; Naselaris et al., 2011; Pearson et al., 2015). While previous studies have investigated the neural regions associated with the generation of mental imagery (Kosslyn & Thompson, 2003; Lee et al., 2012; O’Craven & Kanwisher, 2000; Pearson et al., 2015), and their modulation according to the vividness of that image (Dijkstra, Bosch, & van Gerven, 2017), to our knowledge this is the first study to investigate the neurophysiological measures of the retrieval of previously-encoded mental images, in particular as a function of the vividness of those images at encoding.

Modulations in alpha band oscillations have been found to play a widespread role in human cognition (Başar, 2012; Hanslmayr et al., 2009; Klimesch, 2012; Obleser & Weisz, 2012), including their particular influence on memory functions. In a recent study, Martín-Buro et al. (2020) asked participants to encode pairs of words, perform an old/new recognition task for one word from the pair and then recollect the associated word. They showed that alpha desynchronization increased across the different memory performances (new < old < associated word). More generally, this effect has been seen in an association between both alpha and beta band desynchronization, reflecting the amount of information retrieved from episodic memory (Griffiths et al., 2019; Hanslmayr et al., 2016; Khader & Rösler, 2011; Martín-Buro et al., 2020). This relationship has been interpreted as modulations in alpha/beta band activity promoting the information flow to the neural substrates that represent mnemonic content (Hanslmayr et al., 2012, 2016; Klimesch et al., 2007). As hypothesized, our results mirror this finding, by showing that subjects showed a bigger decrease in alpha activity for successfully remembered items compared to items correctly identified as new.

More critically for our research question, we also observed that items remembered with high confidence that had been rated as highly-vivid during the image generation process at encoding, had an earlier negative peak in alpha oscillations during retrieval compared to mental images that had been rated as low-vivid at encoding but had also been remembered with high confidence. This shifted time course of alpha desynchronization can be interpreted as an earlier memory reinstatement (Griffiths et al., 2019; Hanslmayr et al., 2012, 2016) for the high-vividness items. This result, therefore, provides the first neural evidence in support of the theory from D'Angiulli et al. (2013), based on multiple memory-trace theory (Moscovitch et al., 2016), which postulates that higher vividness is reflective of a greater availability of multiple memory traces in long term memory, thereby enabling both faster image generation and faster retrieval. This latency difference also ramified into an amplitude difference in alpha power from 900 to

1100 ms, as the retrieval process began and completed earlier in time for the high-vividness items.

Our results showed no differences in the magnitude of the parietal old/new ERP effect when comparing the high-vividness to low-vividness items. This is in line with our previous paper (Gjorgieva et al., 2022) analyzing the encoding phase of this experiment, which showed that participants needed a more sustained level of internally-directed attention (as indexed by the steady-state visual evoked potentials that were recorded) to generate low-vividness images that could be successfully later remembered. Additionally, in that study subjects showed a more sustained Dm ERP effect for the subsequently remembered low-vividness items, compared to the successful remembered high-vividness items, suggesting conceptual processing may have been used to compensate for the low-vividness of the mental images at encoding. However, our latency findings suggest that even when low-vivndess items are retrievaed with high confidence, the speed of that memory reinstatement is still slower than the reinstatement for the high-vividness items. Future research is needed to gain further understanding of the neural underpinnings of the vividness-sensitive retrieval processes, as well as other cognitive processes that may help compensate for lower imagery vividness.

We note that our study had an important limitation. Peak latency measures the time at which a peak reaches its maximum (or here minimum) value. Latency measures of electrophysiologically based waveforms tend to be noisier than mean amplitude measures. However, we note that we are applying peak latency to waveform data that was smoothed during the spectral decomposition process, which should eliminate much of the noise in the signal, and our findings clearly support a significant latency difference in the alpha-power changes. Nevertheless, more studies are needed to further assess the differences in latency observed in this study.

In summary, the current study shows that items that were generated with high-vividness at encoding are retrieved from memory more quickly than low-vividness items, even for items that are all remembered with high confidence, and that this process is indexed neurally by the speed of alpha band desynchronization during that retrieval. Accordingly, such results also link the memory retrieval literature with the visual mental imagery literature.

4. Investigating fluctuations of sustained attention and their effects on memory

4.1 Introduction

Sometimes when we are trying to attend to a lecture, we may be distracted by external stimuli, such as people talking in the back of the room, whereas other times, we can be distracted by our own internal thoughts, such as when we daydream about our next meal. Clearly, both external and internal distractors will affect what we can learn from the lecture but they made do so in different ways. Sustained attention (SA) refers to the ability to maintain focus on a task over prolonged periods of time (Esterman & Rothlein, 2019). It is a fundamental cognitive process that directly impacts other cognitive operations, such as learning from a lecture. Fluctuations of SA are commonly observed, but the heterogeneous causes of these fluctuations and the ways in which they influence ongoing information processing and subsequent memory are not well understood. Researchers have subtyped attention by whether it is directed externally towards sensory information or internally towards self-generated information (Chun et al., 2011). In a typical SA task, when individuals are successfully on-task, attention is external and focused. In line with this taxonomy, some researchers propose that SA fluctuations result from a growing tendency towards mind-wandering (shifting attention towards internal distractors) with increasing task duration, due to failure of executive control processes (Thomson et al., 2015). Mind-wandering here is defined as task-unrelated and stimulus-independent thoughts (Stawarczyk, Majerus, Maquet, et al., 2011). Similarly, failures of executive control also allow the capture of attention by external distractors (McVay et al., 2013). The main goal of this study is to investigate the fluctuations of SA and its interaction with subsequent memory.

SA has been typically investigated using variations of the continuous performance task (CPT) and the sustained attention to response task (SART). In these tasks, subjects typically make continuous responses to frequent non-target stimuli and withhold responses to infrequent targets. These continuous responses provide reaction time (RT) data that have been used to index fluctuations in SA. However, the links between RT and SA are unclear, with some studies suggesting lapses in attention can lead to the occurrence of faster RTs due to reflexive errors (Unsworth et al., 2004) and others suggesting that lapses lead to much slower RTs than normal (Unsworth et al., 2010). Other researchers have used moment-to-moment deviations from the mean RT to identify two attention states: (1) an optimal 'in the zone' attention state, defined as periods of low RT variability, associated with higher accuracy and smaller error-related adjustments; and (2) a suboptimal 'out of the zone' state, defined by higher RT variability, associated with lower accuracy and larger error-related adjustments. However, the boundary between the two states is not clear, and the distinction does not clarify the difference between SA lapses due to external distraction vs. mind-wandering and their various causes. Instead, pupillometry measures have been used to investigate this difference in an SA task with intermittent thought probes (Unsworth & Robison, 2016). In comparison to on-task states, mind-wandering states were associated with smaller pretrial baseline pupil diameters while distracted states were associated with larger pretrial baseline pupil diameters. Additionally, task-evoked phasic responses (associated with presentation of the stimuli) were smallest for mind-wandering states and largest when subjects were on-task. Behaviorally, both states were associated with slower RTs. The difference between the on-task and distracted states were not significant. However, the external distractors in this task were 'sights, sounds, temperature, or physical sensations', which are fairly controlled in experimental settings.

In another study investigating the difference between lapses due to external distraction vs. mind-wandering (Stawarczyk, Majerus, Maquet, et al., 2011), during a continuous SART task, researchers presented periodic thought probes asking subjects to indicate if they were (1) on task, (2) off-task due to external distraction, or (3) off-task due to mind-wandering. Participants reported being in an externally distracted state on 20% of all thought probes and mind-wandering on 21%, suggesting both types of executive control failure occurred at similar rates. This study did not compare the rates of external vs. internal distraction over time, however. This is an interesting question because it has been suggested that mind-wandering is the default state and should therefore increase over time as executive control declines due to fatigue (Thomson et al., 2015). At the same time, the decline of executive control over time should be also associated with increased susceptibility to external distraction. Thus, both mind-wandering and external distraction are likely to increase over time. Returning to the learning example, as the lecture goes on and on, we are both likely to be distracted by the voices in the back of the room as well as by our own thoughts. If, instead, mind-wandering increases at a greater rate than external distraction, this could potentially suggest that mind-wandering affords an opportunity for dishabituation, allowing the mind to take a break from the ongoing task and return with refreshed capacity (Schooler et al., 2011).

In addition to examining the causes of these two different types of lapses, it is critical to investigate how they affect ongoing information processing. The closest investigation to this question is a study by (Bonhage et al., 2016), in which subjects were instructed to learn word-pairs while completing a secondary task that was either external (tone discrimination) or internal (monitor their own thoughts). Behaviorally, dividing attention with either the external or internal secondary task led to similar impairments in memory performance. However, the internal secondary task was associated with increased activation of the medial prefrontal cortex (a key node of the default mode network), as well as the anterior cingulate cortex and anterior insula, which are regions that have been linked to performance monitoring (Menon & Uddin, 2010b; Sridharan et al., 2008). In contrast, the secondary external task was associated with reduced activity in the hippocampus, a core memory region. These results suggest that both distractor tasks impaired learning but for different reasons: the external secondary task disrupted basic memory processes (hippocampus) whereas the internal secondary task shifted attention towards internal monitoring (medial prefrontal cortex, anterior cingulate cortex and anterior insula). However, this fMRI study is limited because it did not investigate SA, and attention to the secondary tasks was goal-directed, which is different than spontaneous fluctuations in SA. The current study uses functional MRI (fMRI) to examine spontaneous fluctuations in SA, comparing between lapses in attention due to external distractors or internal distractors (mind-wandering).

Although fMRI studies on SA fluctuations during encoding are not available, one study investigated this question using behavioral methods (deBettencourt et al., 2018). The authors used a version of the SART task (withdraw responses to occasional targets) but with indoor/outdoor scenes. During the SA task, participants pressed a key to a frequent (90%) scene category (e.g., indoor) and withdrew responses to an infrequent (10%) target category (e.g., outdoor). Memory for the scenes was tested with a surprise recognition task. During the SA task, the few trials before a correct target response (withholding response) had slower RTs and were better remembered later, suggesting that higher SA (more careful processing) leads to better learning. In a second experiment, real-time RT fluctuations were used to trigger the infrequent targets when RTs on the preceding 3 trials were 1 SD away from the mean. Memory was worse for scenes triggered by trials that were faster than the mean compared to trials that were slower than the mean, suggesting a causal relationship between attentional state and memory. However, this behavioral study is limited because it did not examine the neural mechanisms underlying interactions between SA and memory.

The aim of the current study was to investigated the neural underpinnings of SA and the influence on subsequent memory. We designed a novel paradigm in which participants viewed a series of trial-unique object images overlaid on top of larger images of faces or houses (alternating between a face and house from trial to trial). The majority of the trials (90%) consisted of a variety of object images and participants were instructed to respond with the same button press on each of these trials. Randomly intermixed throughout were images of toy objects (10%). On trials in which a toy object-image was presented, participants were instructed to respond with an alternate button press.

Attention was indexed across two levels of visual processing. Early visual processing was indexed by fMRI activity in early visual cortex (EVC). Late visual processing was indexed by activity in the lateral occipital complex (LOC) for processing of the object images (Vinberg & Grill-Spector, 2005), fusiform face area (FFA) for processing of the face background images (Kanwisher & Moscovitch, 2000), and parahippocampal place area (PPA) for processing of the house background images (Haxby et al., 2001). Over the course of the task, we predicted that participants would experience failures of SA that could either be due to being distracted by the background images (external distractor) or by internally-generated thoughts (internal distractor). We hypothesized that when participants were attending to the objects, we would observe increased activity in EVC and in regions supporting the processing of the target objects (LOC) but not those supporting the processing of the face or house distractors (FFA and PPA; Gazzaley et al., 2005). When participants were attending to the faces, we expected increased activity in EVC as well as FFA and PPA (Kanwisher & Moscovitch, 2000). Lastly, when participants were mind-wandering, we expected decreased activity in all 3 visual regions (Schooler et al., 2011).

4.2 Methods

4.2.1 Participants

Twenty-six healthy, right-handed young adults (16 women; mean age = 20.67 years, *SD* = 2.14 years) with no disclosed history of neurological or psychiatric episodes participated in the study. Participants provided informed consent and were compensated for their time, in accordance with a protocol approved by the Duke University Institutional Review Board.

4.2.2 Stimuli and procedure

Over the experimental session, participants completed a localizer task, followed by a sustained attention task, and finally, a forced-choice recognition task. The localizer and sustained attention tasks were completed inside of the MRI scanner with stimuli projected onto a mirror at the back of the scanner bore. During the localizer task, participants were presented with a series of images and tasked with making one button response on 90% of trials and an alternate button response when the image was blurred (10% of trials). Responses were recorded using a four-button fiber-optic response box (Current Designs, Philadelphia, PA, USA). The stimuli were images of objects, faces, and houses presented in blocks. The task consisted of 750 trials, which were broken up into 6 blocks of 125 trials (2 blocks per image type). The blocks were pseudorandomly intermixed so that a block of each of the three image types was presented once before the second round. Additionally, two blocks of the same image type could not be presented in a row. Each stimulus was presented for 650 ms with a 350 ms inter-trial internal (ITI). The task took ~14 minutes to complete.

After the localizer task, participants completed the sustained attention task, which consisted of 600 trials broken up into three blocks of 200 trials each. Participants were presented with a series of object images overlaid on top of a larger image of a face or house. Ten percent of the objects were images of toys and participants were tasked with making one button response on the majority of trials (90%) and an alternate button response when a toy object-image was presented (10% of trials). Again, responses were recorded using a four-button fiber-optic response box (Current Designs, Philadelphia, PA, USA). The background images alternated between faces and houses, and participants were instructed to ignore them. Each trial lasted 1000 ms with a 1-4 s (*M* =

2.5s) jittered ITI along a pseudo-exponential distribution. The task took ~35 minutes to complete.

Following the completion of the sustained attention task, participants completed a forced-choice recognition task outside of the MRI scanner. On each trial, participants were presented with each seen object paired with a new object of the same name. Participants selected the seen object while rating their confidence (1 = definitely left to 4 = definitely right). The recognition task consisted of 600 trials broken up into 3 blocks of 200 trials. Participants had up to 2 seconds to respond to each trial, with a 500 ms ITI. The task took ~20 minutes to complete on average.

4.2.3 Behavioral data and analysis

Overall memory performance was evaluated by comparing the hit rate and false alarm rate using a paired sample t-test. Reaction time (RT) data were calculated by averaging the two trials prior to a rare target trial, in which a toy object-stimulus was presented. We compared RTs for trials occurring before a correct vs. error response (pre-error vs. pre-correct) on the rare target trial using a paired sample t-test. Similarly, we calculated the percent of objects remembered for the pre-error and pre-correct trials and compared the conditions using a paired sample t-test.

4.2.4 Pupillometry data and analysis

During the MRI scan, pupil size was recorded continuously with the Eyelink 1000 tracking system, which is MR-compatible (SR Research, Ottawa, Canada), at a 2000

Hz sampling rate. The eye tracker was placed at the end of the scanner bore to track via the head coil mirror. Data were preprocessed and analyzed in MatLab. Missing data due to eye blinks were linearly interpolated. Additional artifacts were detected by thresholding single-trial ranges in pupil size at the 95th percentile, and those trials were excluded (9.8% of trials). Pupil size data were smoothed by calculating the mean of a 200-ms moving window and z-transformed to normalize the data between participants. The prestimulus baseline pupil diameter was extracted by identifying the midpoint of the inter-trial interval and calculating the mean pupil diameter from 250 ms before and after the midpoint. Average pupil size data were compared between conditions using paired sample t-tests.

4.2.5 fMRI data and analysis

MRI data was collected on a General Electric MR750 3T scanner. Scanner noise was reduced using earplugs, and foam pads were used to minimize head motion. The MRI session began with a localizer scan to collect 3-plane (straight axial/coronal/sagittal) localizer faster spin echo (FSE) images. Then the functional images were acquired using a gradient echo-planar imaging (EPI) sequence (TR = 2000 ms, TE = 30 ms, flip angle = 90°, field of view = 192 × 192 mm, 3.0 × 3.0 × 3.0 mm voxels) obtaining 36 oblique slices parallel to the AC-PC line. Functional images were collected in one run for the localizer task and three runs for the SA task. Following the functional runs, we collected a high-resolution structural image (96 axial slices parallel to the AC-PC plane with voxel dimensions of 0.9 × 0.9 × 1.9 mm).

MRI analyses were done using FSL (Jenkinson et al., 2012).The initial six functional images of each run were discarded to allow for scanner equilibrium. The functional images were slice timing corrected, motion corrected, spatially normalized into the Montreal Neurological Institute (MNI) template, and smoothed using an 8-mm FWHM Gaussian kernel. Two participants were excluded from the analysis due to excess motion (greater than the voxel size). Additionally, only trials with correct responses were included in the analysis. Parameter estimates (β values) were calculated from the generalized linear model to assess the magnitude of activation within functionally defined ROIs for each subject. Paired-sample t tests were used to compare parameter estimates between subsequent remembered and forgotten items as well as the fastest and slowest third of RTs and the largest and smallest third of pupil sizes. Subsequently remembered items were constrained to only the high confidence responses.

There were five regions of interests (ROIs) that were functionally defined for each subject. The LOC, FFA, and PPA ROIs were defined using the localizer task by contrasting the object, face, and house regressors, while the EVC and RSC ROIs were defined from using the sustained attention task by contrasting the trial and inter-trial interval regressors. Each ROI was defined as a cluster of seven neighboring voxels within the anatomical structure.

4.3 Results

4.3.1 Behavioral results

Overall, participants made errors on 16.3% of trials in the sustained attention task and subsequently remembered 69.7% of the object images that had been presented. We compared RTs during the sustained attention task for trials prior to a correct or error response (*pre-correct* vs. *pre-*error) on the target trials in which they had to press the alternate button to identify the toy object-image. The RTs were an average of the two trials prior. Using a paired sample t-test, we observed faster RTs on the pre-error (*M* = 830 ms, *SD* = 65) compared to pre-correct trials (*M* = 868 ms, *SD* = 77), *t*(23) = 2.38, *p* = .026, *d* = .49 (**Fig 15A**). Similarly, we compared the percentage of object images remembered during the forced-choice recognition test for pre-error vs. pre-correct trials. Results showed worse subsequent memory for the pre-error (*M* = 76.7, *SD* = 6.1) compared to pre-correct trials (*M* = 80.3, *SD* = 5.7) trials, *t*(23) = -2.19, *p* = .04, *d* = -.45 (**Fig 15B**). These findings suggest that participants were more attentive and/or careful in the trials leading to a correct response compared to the trials prior to an error, resulting in improved memory for those items.

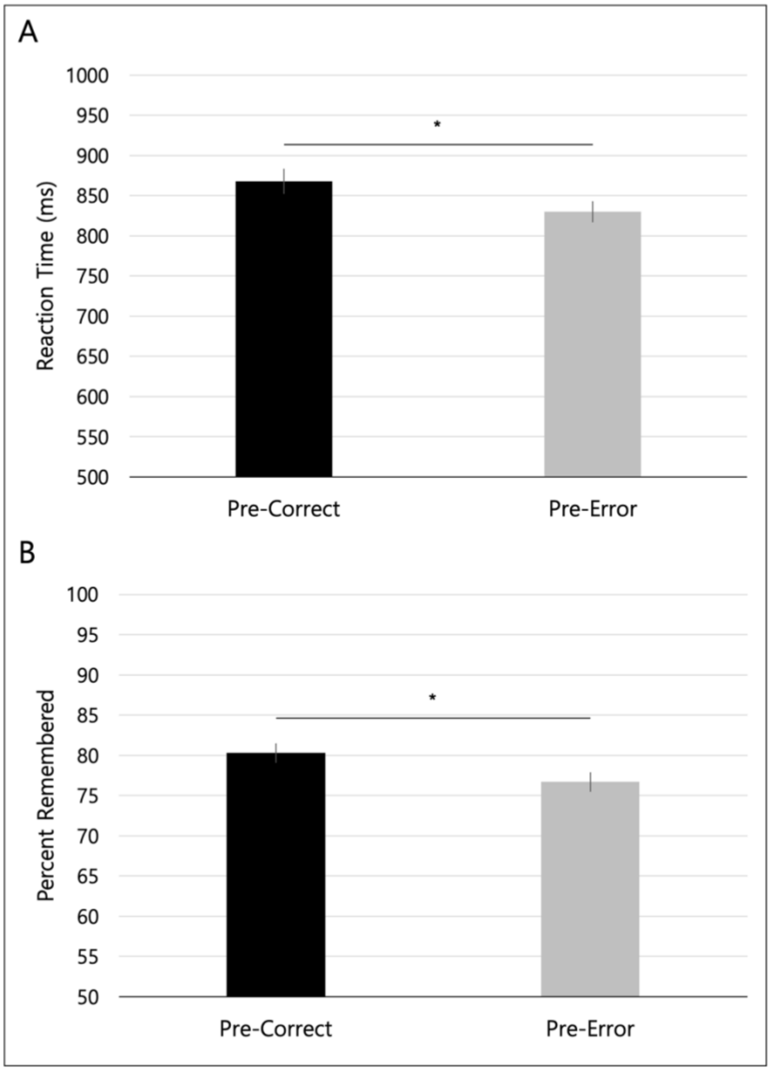

Figure 15: Behavioral results. A) Comparing the pre-correct vs. pre-error trials during the sustained attention test, we observed faster RTs prior to the commission of an error. B) Subsequent memory was worse for trials that occurred prior to an error response compared to a correct response.

4.3.2 Pupillometry results

Pupil size recorded during the inter-trial interval was compared for subsequently remembered vs. subsequently forgotten items using a paired sample t-test. Results showed that larger pupil sizes were observed prior to a trial that was subsequently remembered (*M* = .48, *SD* = .32) compared to forgotten (*M* = .26, *SD* = .33), *t*(23) = 3.45, *p* = .002, *d* = .70 (**Fig 16**), reflecting a more attentive state relative to internally distracted.

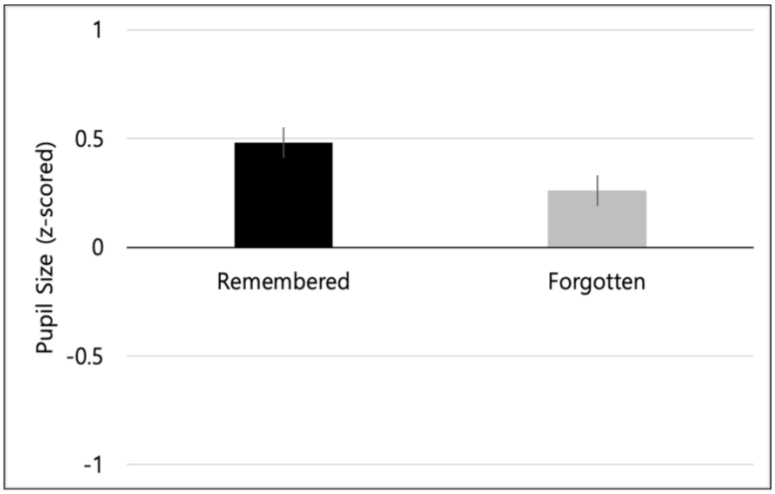

Figure 16: Pupillometry results. Results showed significantly larger pupil sizes in the inter-trial interval prior to subsequently remembered compared to forgotten trials.

4.3.3 fMRI results

fMRI activity was compared in five ROIs: EVC, LOC, FFA, PPA, and RSC. The first four ROIs were selected to index external attention, with EVC measuring lower-order visual processing, LOC measuring higher-order visual processing for the foreground object-images, and FFA and PPA measuring higher-order visual processing for the background images depending on whether the image was a face or house. Only the trials that included a face image were included in the analysis of FFA activation, and only the trials that included a house image were included in the analysis of PPA activation. To investigate differences in activation related to the RTs at encoding, we binned the RT trials into the fastest third and slowest third. Means and standard deviations, as well as the results of the one sample t-tests are presented in **Table 8**. The SLOW > FAST contrast revealed decreased activation in PPA and RSC, suggesting that greater suppression of the external distractor (specifically on the house trials) and internal distractors was related to slower RTs (**Fig 17A**). Similarly, we compared differences in activation based on pupil size by binning the largest third and smallest third. Results from the LARGE > SMALL contrast showed increased activation in EVC (**Fig 17A**). This suggests that differences in pupil size during the inter-trial interval were predictive of EVC activation after the onset of the stimulus, with greater pupil size linked to greater EVC activation.

Finally, we investigated subsequent memory effects by comparing the high confidence subsequently remembered trials to those that were forgotten. Means and standard deviations, as well as the results of the one sample t-tests are presented in **Table 8**. The REM > FORG contrast showed increased activation in LOC and decreased activation in FFA and PPA for the subsequently remembered items (**Fig 17B**). These results suggest that increased attention to the foreground object-image and suppression of the background images were linked to improved memory.

Table 8: fMRI activation means, standard deviations, and t-test results of each ROI for contrasts comparing reaction times, pupil size, and subsequent memory.

Contrast	ROI	Mean (SD)	t	df	p
RT (slow > fast)	EVC	0.81 (3.43)	1.16	23	0.26
	LOC	0.72 (2.99)	1.18	23	0.25
	FFA	0.49 (2.60)	0.92	23	0.36
	PPA	-1.12 (2.16)	2.55	23	0.02*

	RSC	-0.99 (2.25)	2.13	23	0.04*
Pupil (lg > sm)	EVC	0.97 (1.90)	2.49	23	0.02*
	LOC	0.52 (1.81)	1.41	23	0.17
	FFA	-0.61 (2.79)	1.07	23	0.30
	PPA	0.28 (2.01)	0.68	23	0.50
	RSC	-0.89 (3.28)	1.25	23	0.22
Mem (rem > forg)	EVC	0.63 (2.84)	1.09	23	0.29
	LOC	0.91 (1.70)	2.68	23	0.01*
	FFA	-0.89 (1.52)	2.87	23	0.009*
	PPA	-1.26 (2.50)	2.47	23	0.02*
	RSC	-0.54 (2.74)	0.96	23	0.34

*Note:: * indicates p < .05*

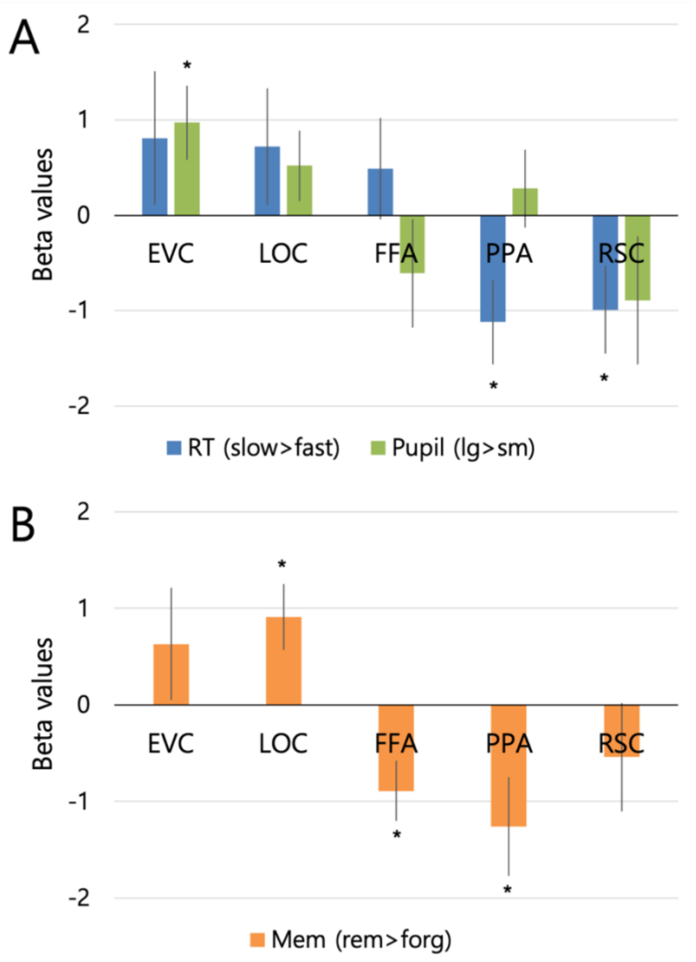

Figure 17: fMRI Results. A) Comparing fMRI activation in the five ROIs based on RTs at encoding showed decreased activation in PPA and RSC when RTs were slower. On the other hand, for the comparison based on pupil size during the ITIs, increased activation in EVC during the stimulus presentation and linked to increased pupil size in the pre-trial interval. Asterisks indicate p < .05. B) Looking at subsequent memory effect activations, we observed increased activation in LOC and decreased activation in FFA and PPA for subsequently remembered items. This suggests that both attention to the foreground object and suppression of the background objects was necessary for successful encoding. Asterisks indicate p < .05.

4.4 Discussion

In the current study, using a combination of fMRI and pupillometry, we investigated SA fluctuations and their influence on subsequent memory. In the encoding phase, a series of object images were presented, each in front of a background image that was randomly a face or house. Participants were instructed to ignore the faces and houses and attend only to the objects, responding with one button press on 90% of trials, and with an alternate button for toy-object images (10% of trials). In the retrieval phase, participants were presented with each object image next to a similar lure, with the task to select the image previously seen and rate their confidence. We observed that slower RTs were associated with decreased activity in PPA and RSC, as well as with improved subsequent memory. Meanwhile, larger pupil sizes were associated with increased activation in EVC and improved subsequent memory. Additionally, for subsequently remembered vs. forgotten item, we observed activation increases in LOC and decreases in the FFA and PPA. Together, these results suggest that suppression of both internal and external distractors was necessary for successful encoding.

Turning to the neural mechanisms of SA, at least three different brain networks are involved: the dorsal attention network (DAN), the default mode network (DMN), and the frontoparietal control network (FPCN). The DAN and the DMN have been associated with external and internal attention, respectively. The DAN, which is composed mainly by dorsolateral prefrontal, bilateral frontal eye fields, and intraparietal sulci regions, is engaged during tasks requiring externally-directed attention (Corbetta & Shulman, 2002). The DMN, which is composed by medial prefrontal, posterior cingulate, and ventral parietal regions (Buckner et al., 2008; Buckner & DiNicola, 2019; Raichle, 2015), exhibits task-induced suppression during external attention tasks (Shulman et al., 1997; Weissman et al., 2006), as well as activation during internal attention, including mind-wandering (Christoff et al., 2009; Mason et al., 2007). The DAN and DMIN tend to be anticorrelated during demanding tasks (Buckner et al., 2008; Fox et al., 2005). Several studies have associated SA lapses with greater DMN activity and weaker DAN activity, as well as with greater connectivity between the two networks (Kucyi et al., 2017; Rothlein et al., 2018). Other studies using mixed methods have found opposite effects (Fortenbaugh et al., 2017) but these results did not replicate in the presence of reward (Esterman et al., 2017), suggesting that it is critical to ensure sufficient motivation during long SA tasks.

The FPCN, which consists of rostrolateral prefrontal cortex, middle frontal gyrus, anterior insula, dorsal anterior cingulate cortex, precuneus, and anterior inferior parietal lobule (Vincent et al., 2008) is associated with cognitive control (Kompus et al., 2009; Ramnani & Owen, 2004). The FPCN is anatomically positioned betwen the DAN and DMN (Vincent et al., 2008), and studies have shown that the FPCN regulates the anti-correlated DMN and DAN (Dixon et al., 2018). In SA tasks, the FPCN has been linked to motivated performance, with subjects proactively engaging this network to reduce attention lapses (Esterman et al., 2017). Thus, the increase in executive control failure over time is associated with decline in FPCN activity over time (Fortenbaugh et al., 2017), as well as reduced DAN-DMN anticorrelation and increased SA lapses. It remains unclear, however, whether reduced FPN activity corresponds to increased mind-wandering, external distraction, or both.

Further analyses are needed to offer insights into the roles of the DAN, DMN, and FPCN in SA. More specifically, a classifier can be trained (via a leave-one-out analysis) on the selective attention localizer task to distinguish between the 3 attention states (attending to the objects, attending to the faces/houses, mind-wandering) within EVC, LOC, and FFA/PPA (Cox & Savoy, 2003). The independently trained classifier can be used to predict patterns in DAN, DMN, and FPN for the SA task according to attentional state and relate those classifications to RT, memory, and pupillometry using a regression approach. Furthermore, a dynamic functional connectivity (dFC) analysis would offer a novel and complementary perspective detailing the interplay within and across networks that gives rise to fluctuations of SA. The nature of SA is intrinsically dynamic and thus dFC can offer unique insights into the network shifts supporting SA.

The current study features novel approaches to both distinguish between different types of SA lapses, as well as to investigate the influence of the individual lapses on subsequent memory. Difficulties in SA have been associated with a wide array of patient populations, including those with ADHD (Li et al., 2012), autism (Corbett et al., 2009), Parkinson's (DeGutis et al., 2016), and Alzheimer's (Berardi et al., 2005). This variety of clinical disorders with these problems underscores the many ways in which the neural mechanisms of SA can be disrupted and lead to higher-level deficits in learning and memory. It remains unclear whether there is a single optimal attention state when sustaining attention, or whether there are multiple cognitive approaches and mechanisms to remain on-task.

5. Learning from mistakes: Incidental encoding reveals a time-dependent enhancement of post-error target processing

5.1 Introduction

Errors are an unavoidable part of life, yet it is commonly remarked that it is not committing an error itself but how we react to it that defines longer-term success. In line with this folk intuition, in the cognitive psychology literature, the capacity to detect an error and use it to adjust subsequent cognitive processing has long been investigated as a possible expression of efficient cognitive control (for recent reviews, see Vidal et al., 2020; Wessel, 2018). However, the exact cascade of cognitive processes that occur after an error remains under debate, including even the fundamental question whether post-error adjustments are adaptive or maladaptive with respect to ongoing task processing (Botvinick et al., 2001; Notebaert et al., 2009). Combined with the fact that aberrant post-error behavior is viewed as a putative marker of impaired cognitive control in assessing clinical populations (Sullivan et al., 2019), a comprehensive understanding of the underlying processes is both of theoretical and practical importance. In the present paper, we argue that the uncertainty surrounding how exactly errors affect subsequent processing stems in large part from limitations in traditional task design and measures. We introduce a novel behavioral paradigm that allowed us to evaluate current models of post-error cognition by tracking the temporal cascade of post-error processing of task-relevant (target) and –irrelevant (distracter) information on a trial-by-trial basis.

5.1.1 Post-error performance: adaptive or maladaptive?

It has long been known that committing an error on relatively fast-paced two-alternative forced choice tasks leads to a reliable slowing of responses on the subsequent trial compared to post-correct trial performance, a phenomenon called post-error slowing (PES; Danielmeier & Ullsperger, 2011; Debener, 2005; Laming, 1968; Rabbitt, 1966). It seems intuitive to conceptualize PES as an adaptive shift in the speed/accuracy tradeoff, that is, people may slow their response following an error in order to avoid a future mistake (Gehring & Fencsik, 2001). This is the essential assumption underlying accounts that view post-error cognition as adaptive. In particular, these views of PES hold that committing an error results in a strategic raising of the response threshold (Botvinick et al., 2001) or enhanced suppression of distracter-induced responding (Ridderinkhof, 2002) on the subsequent trial; these would result in more sensory evidence having to be accumulated to elicit a post-error response (Cavanagh et al., 2011), which in turn promotes slowed but correct actions (Dutilh et al., 2012).

In line with this assumption, a number of studies have observed PES to be accompanied by post-error improvements in accuracy (PIA; Marco-Pallarés et al., 2008; Strozyk & Jentzsch, 2012). Moreover, PES and PIA have been reported to correlate positively across individuals (Hajcak et al., 2003), and PES is particularly pronounced when participants are encouraged to prioritize accuracy over speed (Ullsperger & Szymanowski, 2004). However, other studies have failed to detect any difference between post-error and post-correct trial accuracy (Moran et al., 2015; van den Brink et al., 2014), have not found a within-participant correlation between PES and PIA (Danielmeier et al., 2011), or have even reported a decline in correct responding following errors (Fiehler et al., 2005; Ullsperger & Szymanowski, 2004). Thus, slowing after mistakes is not reliably accompanied by improved accuracy, a fact that seems to undermine the claim that PES, and post-error processing generally, reflects an adaptive, performance-enhancing response to an error.

However, because accuracy is an all-or-none measure, PIA may not be the most sensitive approach to gauging adjustments in post-error processing. An alternative measure of such adjustments is the degree to which distracter stimuli affect post-error response times (RTs). Specifically, post-error processing is commonly assessed in the context of fast-paced selective attention tasks, most notably, variants of the flanker task, where participants are required to categorize a central target stimulus while ignoring flanking distracter stimuli that can be congruent or incongruent with the target (Cavanagh et al., 2011; Debener, 2005; Eichele et al., 2010). This furnishes the researcher with the opportunity to assess the extent to which distracters (i.e., the flankers) influence behavior following correct versus incorrect trials, by comparing response times between incongruent and congruent trials, known as the flanker or interference effect. The size of the flanker effect is taken to reflect the degree of attentional selectivity: a smaller interference effect indicates a stronger focus on the task-relevant stimulus, whereas a larger interference effect indicates a weaker focus.

In line with the idea that post-error processing involves an adaptive re-focusing of attention on task-relevant information, some studies have reported a post-error reduction of interference (PERI) in response time data (King et al., 2010; Ridderinkhof, 2002). However, PERI and PES do not appear to be correlated with each other (King et al., 2010), and subsequent work has suggested that PERI may not actually be a consequence of committing an error per se but rather an expression of adaptation to response conflict inherent in incongruent trials (Borght et al., 2014). Specifically, a majority of errors on the flanker task occur on incongruent trials. A large literature has documented that mean interference effects tend to be reduced following an incongruent compared to a congruent trial (known as the congruency sequence effect, for reviews, see (Duthoo et al., 2014; Egner, 2007), possibly reflecting a conflict-driven enhancement of attentional selectivity (Botvinick et al., 2001). Thus, it may be the case that PERI is a post-incongruent trial effect rather than a post-error adaptation. Van der Borght and colleagues (2014) corroborated this possibility by showing that PERI is in fact conditioned on the congruency of the previous trial, regardless of whether the trial was performed correctly or not. This suggests that PERI may not be a selective expression of post-error cognition, which again casts doubt on post-error processing as an adaptive response.

Perhaps the most challenging finding to the idea of adaptive post-error processing, however, is related to PES itself. In particular, Notebaert and colleagues (2009) showed that manipulating the frequency of error commission substantially influences PES. When errors were rare, PES was observed. However, when correct responses were rare, results showed post-correct trial slowing instead. The authors therefore concluded that slowing of responses after an error does not reflect an error-specific, adaptive processing adjustment, but rather that errors are (typically) considered surprising events that cause a reorienting of attention to that event; this causes a temporary dip in task-focused attention, which in turn delays subsequent task-related processing. Taken together with the inconsistent observation of PIA, the authors suggested that error-triggered changes in processing are in fact maladaptive with respect to ongoing task performance (Notebaert et al., 2009).

5.1.2 The adaptive orienting theory of error processing

In investigating possible determinants of these mixed findings in the literature, (Jentzsch & Dudschig, 2009) reported an important moderating factor on the observation of PES and PIA. In particular, they varied the duration of the response-to-stimulus interval (RSI) between 50 ms and 1000 ms and observed that the short (compared to long) RSI resulted in enhanced PES but reduced PIA (see also (Danielmeier & Ullsperger, 2011). The authors interpreted this pattern as reflecting a processing bottleneck, whereby error processing delays task-related processing (similar to what an orienting response would do). While this particular interpretation has been argued against (e.g., (Houtman & Notebaert, 2013), the basic finding that the timing of the post-error trial is a key factor in determining whether post-error processing appears adaptive or maladaptive has motivated a reevaluation of the literature. In particular, Wessel (2018) has built on these findings to propose a synthesis of (time-dependent) adaptive and maladaptive accounts of post-error processing in the form of the adaptive orienting theory.

According to this proposal, errors are (typically) considered unexpected action outcomes that first trigger an initial automatic, non-specific processing cascade involving rapid inhibition of behavior and cognition to facilitate the orienting of attention to the source of the surprise (here, the error) (see also (Wessel & Aron, 2017). This global inhibition and error-orienting cascade is then followed by error-specific controlled adaptation processes geared at improving task processing; for instance, re-tuning attention to the relevant characteristics of the ongoing task, and adjusting the response threshold. Consequently, the occurrence and nature of PES and PIA will depend on when this post-error processing cascade is interrupted (or probed) by the subsequent trial. If interrupted early (at short RSIs), post-error accuracy will be negatively affected, as attention is oriented towards the source of the error, and task processing is inhibited, but PES will be large, as following the initial inhibition, attention has to be oriented back toward the task (rather than to the source of the error). At slightly longer RSIs, the initial cascade will play out but the adaptive control process is not yet implemented, such that no PIA would occur, and PES would here be driven primarily by a delay in task processing due to having to reorient attention from the error source to the ongoing task. At even longer RSIs, the cascade is not interrupted, such that a PIA, PERI, and PES should be observed, and in this case, these would in part reflect a strategic change in processing, such as re-tuning attention to the task at hand. A recent study by Li and colleagues (2020) used EEG to investigate post-error processing at a short (200 ms) versus long RSI (1000 ms). At the short RSI, EEG markers indicated dampened sensory processing, enhanced motor inhibition, and an absence of attentional adjustments on post-error compared to post-correct trials. By contrast, in the long RSI condition, no differences in markers of sensory processing, but a facilitation of motor processing, and attentional adjustments were observed. These findings provide support for the idea that task processing is impaired shortly after error commission, but improved if given more time, in line with the adaptive orienting theory. However, this study did neither allow the authors to assess post-error adjustments on a trial-by-trial level, nor to selectively assess processing of targets versus distracters.

While Wessel's (2018) adaptive orienting theory represents an elegant reconciliation of diverse prior findings and proposals on PES, PIA, and PERI, direct tests of the model's proposed processing cascade are currently lacking. First, few prior studies have assessed post-error performance indices across more than two RSIs.

Second, and more importantly, the indices of post-error cognition used in the prior literature have a number of key limitations. Specifically, in addition to the issues raised above about the reliability and provenance (or selectivity) of PIA, PERI, and PES, an additional major drawback in interpreting these metrics is that they represent aggregate measures of performance, relying on averaging data over many trials. For instance, a given trial is either correct or incorrect, and PIA cannot tell us anything about how task stimuli are processed on correct post-error trials. Similarly, PES and PERI reflect averaged difference scores between different trial types, and thus do not allow one to measure cognitive processing on individual post-error trials. In order to evaluate the adaptive orienting account with greater sensitivity, we here developed a novel approach that allowed us to gauge post-error cognition on a trial-by-trial basis.

5.1.3 The current study

To trace post-error cognition with greater sensitivity than previous studies, we here introduce a novel approach that measures post-error stimulus encoding at the single trial level. This is achieved by employing a flanker task that uses trial-unique object images as targets and flankers, and which is followed - after a brief filler task providing an encoding-retrieval interval - by a surprise recognition memory test for both the target and flanking stimuli. This approach thus allowed us to gauge the degree of on-task focus - or attentional selectivity - on each trial, as reflected by (incidental) encoding of target relative to flanker stimuli. With respect to assessing the adaptive orienting model, we could thus measure the degree of on-task focus on a trial-by-trial level, and compare attentional selectivity between post-correct and post-error trials as a function of RSI duration (here, 300 ms vs. 650 ms vs. ~1000 ms). We used this approach to test the proposal that post-error processing transitions from an early orienting response (which should result in poor processing of task-relevant stimuli at short RSIs) to subsequent adaptive re-focusing of attention to the task (which should be reflected in enhanced processing of task-relevant stimuli at long RSIs).

5.2 Experiment 1

Experiment 1 introduces our novel task protocol and employed a relatively long RSI (~1000ms) that, based on the adaptive orienting account, would be expected to result in adaptive post-error processing. The protocol consisted of an object-based flanker task using trial-unique images, followed by a surprise recognition memory test that allowed us to measure the trial-wise selectivity of incidental stimulus encoding. Here, adaptive post-error processing would be reflected in improved memory for target (but not distracter) objects following error as compared to correct trials.

5.2.1 Methods

5.2.1.1 Participants

For all experiments, participants were recruited from Amazon Mechanical Turk's (MTurk) online platform and provided informed consent in accordance with Duke University's Institutional Review Board. We aimed for a sample of ~100 valid participants, as previous studies have reported relatively small effect sizes for post-error slowing (e.g., Hajcak et al., 2003), and we expected a correspondingly small effect size for potential differences in incidental memory. Therefore, for all experiments, we ran participants in batches of N=9 and stopped once we obtained 100+/- 5 valid participants, based on the below exclusion criteria. For Experiment 1, a total of 126 participants (age: M = 31.2, SD = 3.2; 52 female) were recruited. Participants were excluded if they did not complete the full experiment (N = 2) or if their error rate was less than 10% (N = 4). Additionally, we defined two exclusionary criteria based on accuracy. To ensure that participants were engaged with the task, we excluded anyone with a flanker task accuracy at or near chance (<55% accuracy, N = 0). Furthermore, since we were interested in within-subject differences in memory strength for post-error vs post-correct targets and flankers, we did not want the assessment of such differences to be confounded by floor effects, so we also excluded participants whose memory performance was at or near chance, with a hit rate below 55% (N = 12). Finally, for the memory analyses, we additionally excluded participants if over 30% of flanker task errors occurred as multiples in a row (N = 8). The memory analyses compared memory data from correct trials only. Therefore, participants who committed a substantial proportion of errors in sequence would leave too few usable post-error trials. The final sample size was 108 for the flanker analyses and 100 for the memory analyses.

5.2.1.2 Stimuli and procedure

The protocol consisted of a modified flanker task with trial-unique object images followed by a surprise memory test. In the flanker task, participants were presented with a central living or non-living object image (the target) flanked on both sides by a second living or non-living object (the distracter, see **Fig. 18** for an example trial). The images were obtained from the CabezaLabObjects database, and had been normed for familiarity. Living object images consisted of animals and plants, while non-living object images consisted of tools, musical instruments, vehicles, and household items (i.e., furniture, electronics, etc.). All images were presented in color at 85×85 pixels.

The flanker task consisted of 120 trials, each lasting 1800 ms. Each trial began with the presentation of the flanking object presented for 200 ms before the target object was added in the center. Both objects remained on the screen until a response was made, up to 800 ms, followed by another 800 ms fixation. Unlike in the subsequent experiments, in Experiment 1 the RSI was not directly controlled but – given the above timing parameters - was expected to average around 1000 ms based on pilot data RTs. In the actual Experiment 1 data set, the average RTs between subjects ranged from 527-889 ms (M = 660, SD = 59), resulting in an RSI range of 711-1073 ms, with a mean of 940 ms. On congruent trials, both the target image and flanking image were either living or non-living. On incongruent trials, one image was living while the other was non-living. Participants were instructed to categorize the central target image according to living/non-living categories as fast as possible while being accurate. Responses were given via a keyboard “J” or “K” button press, with the button-category mapping counter-balanced across subjects. Over the course of the flanker task, 240 trial-unique images were presented (120 targets, 120 flankers).

After completing the flanker task, participants filled out a demographic questionnaire, which created an encoding-retrieval interval of about 5-6 min. They were then instructed to perform a surprise memory test. Here, they were presented with the 240 images they had previously seen, randomly intermixed with 120 new images, for a total of 360 trials. Images were presented one at a time for up to 3 s or until a response was recorded. Participants were instructed to determine for each image whether it was old (previously seen in the flanker task) or new, and rate their confidence from 1 (definitely new) to 6 (definitely old) using the keyboard number pad.

5.2.1.3 Flanker task analyses

In terms of performance accuracy, we compared accuracy rates between incongruent and congruent trials using a paired sample t-test, expecting greater error rates for incongruent trials (i.e., a flanker interference effect). To test for post-error improvements in accuracy (PIA), we calculated mean accuracy rates for trials following a correct response and trials following an incorrect response. Accuracy data were submitted to a paired sample t-test. We analyzed the reaction time (RT) data to evaluate interference effects, post-error slowing (PES), and post-error reduction of interference

(PERI). RT data were submitted to a 2 (congruency: congruent vs. incongruent) × 2 (trial type: post-correct vs. post-error) repeated-measures analysis of variance (rANOVA). We expected a main effect of congruency, whereby slower RTs on incongruent than congruent trials would replicate typical flanker interference effects, as well as a main effect of trial type, with slower RTs for post-error trials reflecting PES. Lastly, the interaction between congruency × trial type, with a smaller incongruent-congruent RT difference for post-error vs post-correct trials, would indicate a PERI effect.

5.2.1.4 Incidental memory test analyses

First, we confirmed that incidental memory was above chance with a t-test comparing the hit rate with the false alarm rate. Then, hit rate data were submitted to a 2 (stimulus feature: target vs. flanker) × 2 (trial type: post-correct vs. post-error) rANOVA to provide the crucial test of how post-error processing affects the encoding of target and/or distracter objects. Based on a large literature on attention facilitating encoding, we expected a main effect of stimulus feature, with better memory for the targets in comparison to the flankers, as reflected by an increased hit rate for targets. If post-error processing with a long RSI were adaptive, we would also expect improved target stimulus memory for the post-error vs post-correct trials; if it were maladaptive, memory would be worse for post-error targets. Critically, the interaction between trial type × stimulus feature allowed us to test for a change in attentional selectivity following an error: if memory were selectively improved for post-error targets, this would provide direct evidence for adaptive accounts of post-error processing. We include Bayes Factors for all memory results, using the BFEffects R Package (https://github.com/mattansb/BFEffects).

To confirm the reliability of the confidence ratings, data were submitted to paired sample t-tests to compare mean confidence levels based on accuracy: correctly remembered (hits) vs forgotten items (misses) and correctly identified new (correct rejections) vs incorrectly identified new items (false alarms). As an additional measure of trial-level post-error stimulus encoding, we compared the memory confidence ratings between post-error and post-correct trials, where higher confidence ratings correspond to better memory. To determine selective memory improvement, we compared the difference between confidence ratings for the target minus flanker stimulus within each trial. Adaptive post-error processing would be reflected in a greater memory advantage (higher confidence) for the targets over flankers on post-error compared to post-correct trials.

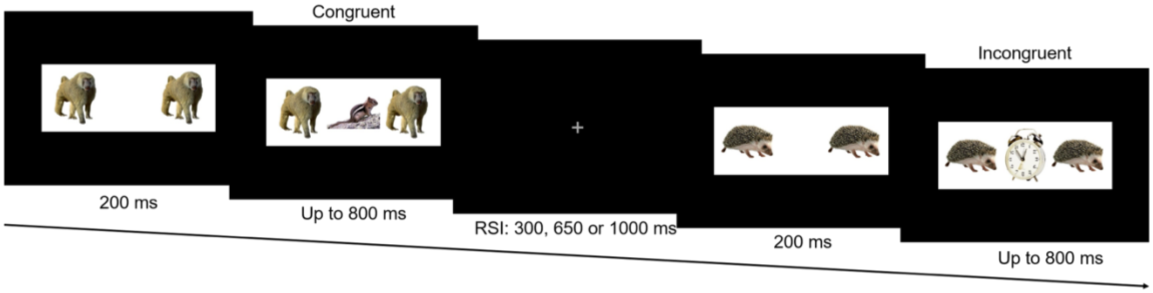

Figure 18: Flanker task paradigm. Each trial began with the presentation of the flanker stimuli for 200 ms, followed by the target. Participants were instructed to categorize the target stimulus as living or non-living, and the objects remained on the

screen for up to 800 ms or until the response. The RSI (300, 650, or, ~1000) was varied between three experiments.

5.2.2 Results

5.2.2.1 Flanker task

Participants committed errors on 21.0% of trials, with more errors occurring on incongruent (M = 11.7, SD = 1.9) compared to congruent trials (M = 9.4, SD = 2.6), t(107) = 7.67, p < .001, d = .74. In line with previous PIA results, we observed an improvement in accuracy for post-error (M = 79.9, SD = 4.7) compared to post-correct (M = 77.8, SD = 2.7) trials, t(107) = 4.30, p < .001, d = .41. **Table 9** displays means and standard deviations for the RT data, and **Figure 19** visualizes congruency and PES effects. RT data were submitted to a 2 × 2 rANOVA. In line with typical flanker interference effects, there was a main effect of congruency, F(1,107) = 4.60, p < .05, np2 = .04. RTs were slower for incongruent (M = 669, SD = 64) compared to congruent (M = 651, SD = 64) trials. Moreover, there was a main effect of trial type reflecting PES, with significant RT slowing for post-error (M = 700, SD = 83) compared to post-correct (M = 649, SD = 61) trials, F(1,107) = 50.74, p < .001, np2 = .32. Finally, we observed a significant interaction between congruency and trial type, F(1,107) = 9.30, p < .003, np2 = .08. Post hoc Bonferroni-corrected pairwise comparisons indicated a PERI effect; the incongruent-congruent RT difference was smaller for post-error, t(107) = -1.17, p > .05, d = -.11, compared to post-correct, t(107) = 2.92, p < .005, d = .28, trials.

Table 9: Response time (ms) means and standard deviations during flanker task for each experiment.

Trial Type	Experiment/RSI	Post-Correct	Post-Error
Congruent	*Exp 1: ~1000 ms RSI*	641 (68)	703 (80)
	Exp 3: 650 ms RSI	649 (54)	676 (54)
	Exp 2: 300 ms RSI	689 (59)	698 (66)
Incongruent	*Exp 1: ~1000 ms RSI*	659 (70)	699 (87)
	Exp 3: 650 ms RSI	662 (58)	680 (57)
	Exp 2: 300 ms RSI	713 (53)	725 (51)

5.2.2.2 Incidental memory

Table 10 displays means and standard deviations for the memory data. Overall memory performance was well above chance, with a mean hit rate of 63.5% and false alarm rate of 30.4%, t(99) = 48.32, p < .001, d = 4.83. (Note that above-chance performance was of course expected, based on our exclusion criteria). Additionally, confidence ratings were greater for hits (M = 5.02, SD = .44) compared to misses (M = 4.83, SD = .40), t(99) = 3.43, p < .001, d = .34, as well as correct rejections (M = 2.15, SD = .24) compared to false alarms (M = 2.69, SD = .23), |t| = 3.71, p<.01, d = .56, indicating higher confidence for correct memory judgments. Hit rate data were submitted to a 2 × 2 rANOVA. There was a main effect of trial type, such that objects from post-error trials were better remembered (M = 66.6, SD = 5.9) than those from post-correct trials (M = 62.7, SD = 7.0), F(1,99) = 38.12, p < .001, np2 = .28, BF = 7.38×104. This result was echoed by higher memory confidence ratings for images from post-error (M = 5.4, SD = 0.9) vs. post-correct (M = 4.7, SD = 0.7) trials (|t| = 2.04, p<.05, d = .43). Additionally, there was a main effect of stimulus feature, with better memory observed for the target (M = 70.0, SD = 7.5) than the flanker images (M = 57.0, SD = 7.7), F(1,99) = 358.64, p < .001, np2 = .78, BF = 3.28×1057. Critically, these effects were qualified by an interaction between trial type × stimulus feature, F(1,99) = 27.07, p < .001, np2 = .21, BF = 1.25×104. Post hoc Holm-corrected pairwise comparisons showed significantly improved post-error compared to post-correct memory for the targets, |t| = 8.02, p < .001, but not for flankers, |t| = .45, p > .05. Moreover, the difference in confidence ratings between the target and flanker stimuli within each trial was larger for post-error (M = 2.7, SD = .3) compared to post-correct (M = 2.0, SD = .3) trials, |t| = 6.43, p<.001, d = .57.

Table 10: Means and standard deviations for percent of stimuli remembered in each experiment.

Trial Type	Experiment/RSI	Post-Correct	Post-Error
Target	*Exp 1: ~1000 ms RSI*	68.4% (9.0)	75.8% (7.0)
	Exp 3: 650 ms RSI	66.3% (8.2)	71.2% (8.3)
	Exp 2: 300 ms RSI	64.9% (8.1)	66.6% (8.6)
Flanker	*Exp 1: ~1000 ms RSI*	57.0% (8.2)	57.4% (8.7)
	Exp 3: 650 ms RSI	58.7% (5.0)	59.1% (5.9)
	Exp 2: 300 ms RSI	56.9% (5.9)	57.0% (5.3)

5.2.3 Discussion

In sum, the newly developed flanker protocol with trial-unique objects reproduced the hallmark effects: robust flanker interference and significant PES, PIA, and PERI effects. These data provided a strong foundation for the assessment of how post-error processing affects the incidental encoding of target and distracter stimuli. With respect to the latter, we observed a novel effect: a selective memory enhancement for post-error targets. For brevity, we will here refer to this effect as post-error target enhancement (abbreviated as PETE). This finding of enhanced attentional selectivity following error trials clearly supports the notion of adaptive, goal-conducive post-error adjustments in cognitive processing at a relatively long RSI of ~1000ms.

5.3 Experiment 2

Having demonstrated adaptive post-error processing via incidental encoding at a long RSI, we next turned to employing our new trial-wise measure of encoding selectivity to assess how error-triggered adaptation of cognitive processes varies as a function of RSI duration. Specifically, according to the adaptive orienting account, one would expect poor task stimulus processing (i.e., no post-error encoding benefits) early after error occurrence (i.e., at very short RSIs), but for enhanced target processing to emerge at longer RSIs. Experiments 2 and 3 were designed to plot out this hypothesized time-course of post-error processing by examining incidental stimulus encoding at short (Experiment 2: 300ms) and medium duration RSIs (Experiment 3: 650ms). Thus, in Experiment 2, we time-locked the onset of each target to occur 300 ms after the response from the previous trial. We hypothesized that presenting the next trial so soon after the erroneous response would tap into the initial orienting of attention towards the source of the error. Thus, we expected to observe post-error slowing in the absence of any post-error improvements in target encoding.

5.3.1 Methods

5.3.1.1 Participants

The recruitment target and procedure were identical to Experiment 1. This resulted in recruiting 144 participants who provided informed consent in accordance with Duke University's Institutional Review Board (age: M = 36.8, SD = 4.0; 68 female). Once again, participants were excluded if they did not complete the full experiment (N = 3), if their error rate was less than 10% (N = 6), or if accuracy (N = 0) or memory (N = 16) was at chance. Four participants were excluded due to technical issues. In addition, participants were excluded from the memory analyses if over 30% of errors occurred as multiples in a row (N = 19). The final sample size was 115 for the flanker analyses and 96 for the memory analyses.

5.3.1.2 Stimuli and procedure

The task was the same as in Experiment 1, except that the onset of each target was time-locked to occur 300 ms after the participant's response in the previous trial.

5.3.1.3 Analyses

The analyses were the same as in Experiment 1.

5.3.2 Results

5.3.2.1 Flanker task

The mean error rate was 26.6%, with more errors occurring on incongruent (M = 14.5, SD = 2.9) rather than congruent trials (M = 12.2, SD = 4.1), t(114) = 4.05, p < .001, d =

.38. There was improved accuracy for post-correct (M = 73.2, SD = 3.2) vs post-error trials (M = 72.3, SD = 3.5), t(114) = -2.76, p < .01, d= -.26. **Table 9** displays means and standard deviations for the RT data, and **Figure 19** visualizes congruency and PES effects. In the RT data, we observed both a main effect of congruency, F(1,114) = 8.20, p < .005, np2 = .07, with slower RTs for incongruent (M = 717, SD = 45) compared to congruent (M = 691, SD = 55) trials, and a main effect of trial type, F(1,114) = 47.77, p < .001, np2 = .30. Post-error trials had slower RTs (M = 715, SD = 46) than post-correct trials (M = 700, SD = 52). However, with an RSI of 300ms, there was no interaction between trial type and congruency, F(1,114) = .15, p > .05, np2 = .001, that is, we detected no PERI effect.

5.3.2.2 Incidental memory

Table 10 displays means and standard deviations for the memory data. As expected, memory was above chance, with a hit rate of 58.7% and a false alarm rate of 28.9%, t(95) = 44.69, p < .001, d = 4.56. Similar to Exp 1, confidence ratings were greater for hits (M = 4.97, SD = .23) compared to misses (M = 4.42, SD = .23), |t| = 3.43, p<.05, d = .42, as well as correct rejections (M = 2.42, SD = .21) compared to false alarms (M = 2.71, SD = .27), |t| = 3.32, p<.02, d = .37, indicating higher confidence for correct memory judgments. We observed no main effect of trial type, F(1,95) = 3.54, p > .05, np2 = .04, BF = .38, with no difference between post-correct (M = 60.9, SD = 6.2) and post-error (M = 61.8, SD = 5.7) trials. However, there was a main effect of stimulus feature, as target stimuli (M = 65.4, SD = 7.6) were better remembered than flanker stimuli (M = 54.7, SD =

5.1), F(1,95) = 180.10, p < .001, np2 = .66, BF = 2.05×1040. Critically, there was no interaction between trial type and stimulus feature, F(1,95) = 2.98, p > .05, np2 = .03, BF = .43. This PETE null-effect extended to the confidence ratings between the target and flanker on each trial, with no significant differences observed for post-error (M = 2.0, SD = 0.3) vs. post-correct (M = 1.9, SD = 0.4) trials, |t| = 1.28, p>.05, d = .14.

5.3.3 Discussion

Similar to Experiment 1, we observed typical flanker interference as well as PES effects. However, with an RSI of 300ms, we detected no PERI effect and no PIA effect. Moreover, we detected no post-error improvements in memory for either the targets or the flankers. These results are in line with the idea that early processing following an error does not involve enhanced target encoding, in spite of overall slower responses compared to post-correct trials. We next probed whether enhanced encoding selectivity effects of post-error processing would emerge at medium duration RSIs.

5.4 Experiment 3

To further characterize the time-course of post-error processing, we ran a third experiment with an RSI of 650ms, equidistant between 300 and 1000ms. At a 650ms RSI, we hypothesized that early adaptive processing (following the initial orienting response) would be taking place, leading to a PETE effect, but of a smaller size than that observed at an even longer RSI in Experiment 1.

5.4.1 Methods

5.4.1.1 Participants

The recruitment target and procedure were identical to Experiment 1. This resulted in recruiting 126 participants from MTurk, who provided informed consent in accordance with Duke University's Institutional Review Board (age: M = 34.2, SD = 3.7; 61 female). Once again, participants were excluded if their error rate was less than 10% (N = 7) or if accuracy (N = 0) or memory was at chance (N = 9). The final sample size was 108 for the flanker analyses and 99 for the memory analyses.

5.4.1.2 Stimuli and procedure

The task was the same as in Experiment 1 and 2, except that the onset of each target was time-locked to occur 650 ms after the participant's response in the previous trial.

5.4.1.3 Analyses

The analyses were the same as in Experiments 1 and 2.

5.4.2 Results

5.4.2.1 Flanker task

Participants committed errors on 22.2% of trials, with a larger contribution from incongruent (M = 12.8, SD = 2.3) compared to congruent trials (M = 9.4, SD = 5.4), t(107) = 5.38, $p < .001$, d = .52. Unlike Exp 1, we did not observe a PIA effect. There was no difference in accuracy between post-error (M = 77.5, SD = 5.8) and post-correct trials (M =

77.3, SD = 5.9), t(107) = 1.48, p > .05, d = .14. **Table 9** displays means and standard deviations for the RT data, and **Figure 19** visualizes congruency and PES effects. As in Experiments 1 and 2, the RT data revealed a main effect of congruency, as RTs were slower for incongruent (M = 667, SD = 56) than for congruent (M = 655, SD = 53) trials, F(1,107) = 11.19, p < .001, np2 = .10. Furthermore, there was a main effect of trial type, F(1,107) = 81.66, p < .001, np2 = .43, with slower RTs for post-error (M = 678, SD = 54) than for post-correct (M = 655, SD = 54) trials, i.e., PES. Finally, we observed a significant interaction of congruency × trial type, F(1,107) = 5.92, p < .02, d = .05, replicating the PERI effect observed in Experiment 1. The incongruent-congruent RT difference was smaller for post-error, t(107) = 1.38, p > .05, d = .13, compared to post-correct, t(107) = 4.23, p < .001, d = .41, trials.

5.4.2.2 Incidental memory

Table 10 displays means and standard deviations for the memory data. As expected, overall memory performance was above chance, with a hit rate of 63.1% and a false alarm rate of 24.2%, t(98) = 69.98, p < .001, d = 7.03). Additionally, confidence ratings were greater for hits (M = 4.97, SD = .25) compared to misses (M = 4.70, SD = .23), |t| = 3.43, p<.05, d = .41, as well as correct rejections (M = 2.22, SD = .20) compared to false alarms (M = 2.65, SD = .25), |t| = 3.31, p<.02, d = .45, indicating increased confidence for correct memory judgments. There was a main effect of trial type, F(1,98) = 22.74, p < .001, np2 = .19, BF = 292.40, due to better memory for stimuli from post-error trials (M =

65.2, SD = 5.4) than for those from post-correct trials (M = 62.5, SD = 4.9). Similarly, confidence ratings were higher for objects from post-error (M = 5.4, SD = 1.0) compared to those from post-correct trials (M = 4.7, SD = 0.8) (|t| = 5.37, p<.001, d = .56). There was a main effect of stimulus feature, as well, with better memory for the target (M = 67.4, SD = 7.0) than the flanker images (M = 58.8, SD = 4.6), F(1,98) = 218.04, p < .001, np2 = .69, BF = 2.30×1037. Crucially, as in Experiment 1, these effects were qualified by an interaction of trial type × stimulus feature, F(1,98) = 11.09, p = .001, np2 = .10, i.e., the PETE effect. Post hoc Holm-corrected pairwise comparisons showed significantly improved post-error compared to post-correct memory for the target objects |t| = 5.59, p < .001, but not for flankers |t| = .43, p > .05. Extending these findings of enhanced post-error encoding selectivity, the difference in confidence ratings between the target and flanker stimuli within each trial was also larger for post-error (M = 2.2, SD = 0.4) compared to post-correct (M = 1.9, SD = 0.4) trials, |t| = 5.27, p<.001, d = .51.

5.4.3 Discussion

The results of Experiment 3 again replicated classic interference and PES effects (summarized across all three experiments in **Fig. 19**). Beyond that, with a 650ms RSI, we replicated the PERI effect and – most importantly, the PETE effect, that is, the selective post-error improvement in memory for target stimuli observed with a ~1000ms RSI in Experiment 1. As in Experiment 2, no PIA was detected, however. These results demonstrate that, within the context of this task, by 650ms after committing an error, post-error processing is already adaptive in nature. In line with the proposal that processing moves from initial orienting to subsequent adaptive adjustments, and that the implementation of the latter takes some time, the degree of the selective target encoding effects we observed were non-existent at 300ms RSI, and numerically larger at ~1000ms than at 650ms RSI (**Fig. 20**). To formally test for a time-dependent change in target stimulus encoding, we next conducted a cross-experiment analysis.

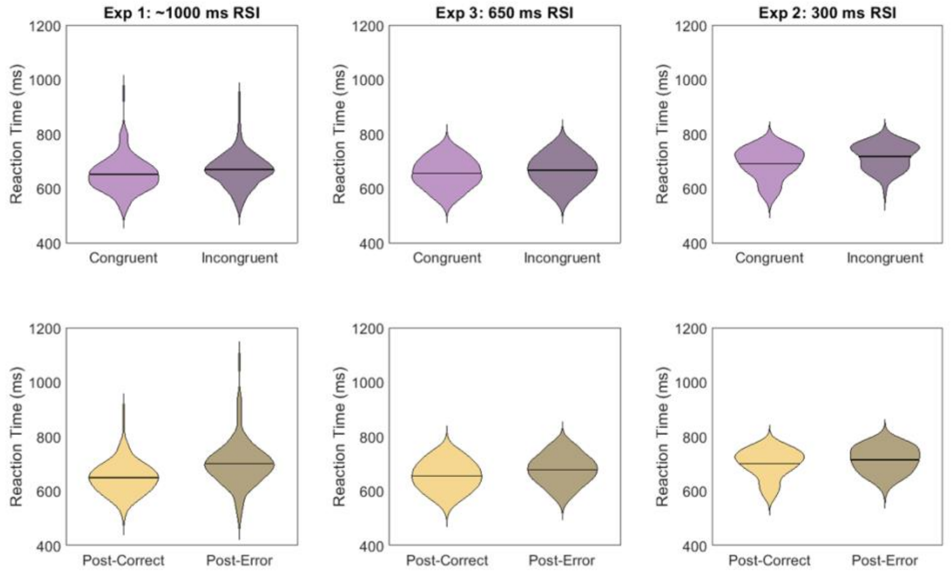

Figure 19: Flanker task response time (RT) data. Mean RT (indicated by the black line) and RT distributions (violin plots) are shown for congruent versus incongruent trials (top panels), showing a typical flanker congruency or interference effect; and for post-correct versus post-error trials (bottom panels), showing a classic post-error slowing effect.

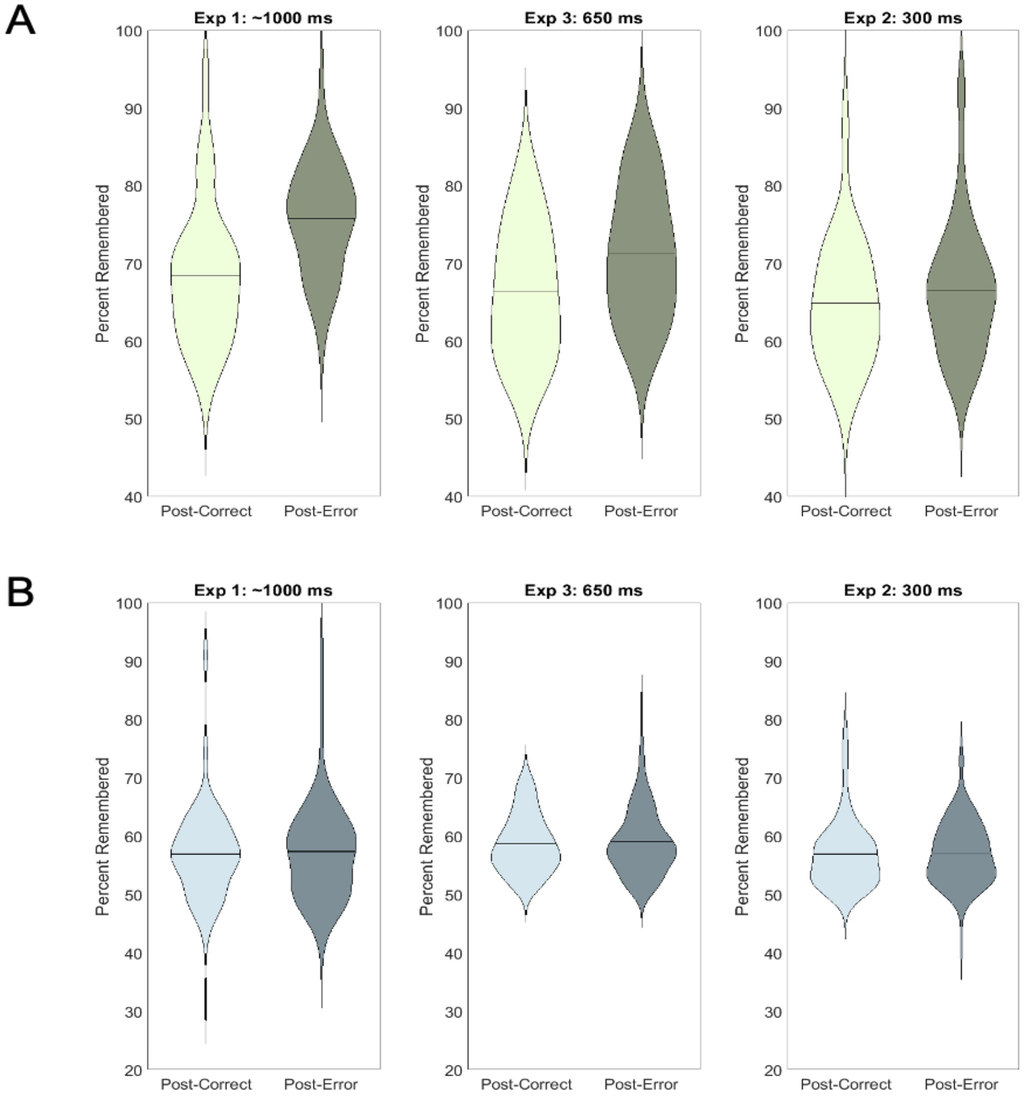

Figure 20: Memory task hit rate data. A) The mean percentage of correctly recognized target stimuli (black lines) and distribution (violin plots) are shown as a function of post-correct versus post-error trials. A target-specific improvement in memory was observed for post-error trials at the long RSIs (650 ms, 1000 ms), but not the short RSI (300 ms). This memory improvement increased as a function of RSI length, with the 1000 ms RSI experiment resulting in the largest memory improvement. B) The mean percentage of correctly recognized flanker stimuli (black lines) and distribution (violin plots) are shown as a function of post-correct versus post-error trials. No memory improvement was observed for post-error compared to post-correct trials.

5.5 Cross-experiment analysis

To directly compare PETE across experiments, hit rate difference scores (post-error minus post-correct) were submitted to a 3 (between subjects RSI: long vs. medium vs. short) × 2 (stimulus feature: target vs. flanker) rANOVA. The data are displayed in **Figure 20**. There was a between subjects effect of RSI, $F(1,2) = 7.69$, $p < .001$, np2 = .05, BF = 6.87. Additionally, there was a within subjects effect of stimulus type, $F(1,1) = 37.81$, $p < .001$, np2 = .12, BF = 1.53×108, and an interaction between RSI and stimulus type, $F(1,2) = 4.86$, $p = .008$, np2 = .03, BF = 7.18.

To determine the source of the interaction, data were submitted to two 3 (between subjects RSI: short vs. medium vs. long) × 1 ANOVAs, one for the target stimuli and one for the flanker stimuli. There was an effect of RSI for the target stimuli, $F(1,2) = 8.98$, $p < .001$, np2 = .06. Post hoc Holm-corrected comparisons showed a larger target-specific memory improvement for post-error compared to post-correct trials when the RSI was ~1000 ms ($M = 7.4$, $SD = 10.4$) vs. 300 ms ($M = 1.6$, $SD = 7.0$), $t = 4.23$, $p < .001$, $d = .65$. Similarly, we observed a larger target-specific memory improvement for post-error compared to post-correct trials when the RSI was 650 ms ($M = 4.9$, $SD = 10.6$) compared to 300 ms, $t = 2.39$, $p = .035$, $d = .36$. The difference between the ~1000 ms and 650 ms RSI was trending, $t = 1.84$, $p = .066$, $d = .24$. There was no effect of RSI for the flanker stimuli, $F(1,2) = .08$, $p > .05$, np2 = 5.67×10-4.

In sum, the cross-experiment analysis supports a time-dependent emergence of adaptive post-error processing, as reflected in target-selective encoding benefits, with no beneficial encoding effects when stimuli are presented 300ms after an erroneous response, and significant benefits emerging at 650ms and growing further at a ~1000ms RSI. Our favored interpretation of the PETE effects in Experiments 1 and 3 (RSIs: ~1000ms and 650ms) is that, in line with the adaptive orienting account, committing an error triggers an initial stopping and orienting towards the source of the error, followed by a refocusing on the task-relevant stimulus feature. However, in the following we also consider alternative interpretations that do not depend on the assumption that committing an error is the key factor in producing enhanced post-error target encoding.

5.6 Control analysis

First, there are two possible ways in which memory could have been driven by stimulus congruency rather than errors. On the one hand, some previous studies have found memory for target stimuli to be enhanced for incongruent compared to congruent trials (e.g., Krebs et al., 2015). Perhaps, by chance, post-error trials in the present study were predominantly incongruent trials, in turn resulting in better target memory. To assess this possibility, we examined the rates of incongruent stimuli for post-error vs post-correct trials. There were no differences in the proportion of incongruent stimuli that occurred on post-error (Experiment 1: M = 43.9, SD = 1.9; Experiment 3: M = 46.0, SD = 2.3) vs. post-correct (Experiment 1: M = 46.1, SD = 1.7; Experiment 3: M = 44.3, SD = 1.9) trials in either experiment (Experiment 1, |t| = .41, p>.05, Experiment 3, |t| = .35, p>.05). On the other hand, as noted in the Introduction in the context of PERI, the majority of errors in the type of task employed here tend to be committed on incongruent trials. It is therefore possible that the memory effects observed in Experiments 1 and 3 really reflect trial-by-trial adaptation processes in response to conflict elicited by incongruent stimuli rather than to errors per se. To test the plausibility of this alternative account, we used a paired sample t-test to compare memory for the target on post-incongruent vs post-congruent trials for Experiments 1 and 3. There were no differences in target memory on post-incongruent (Experiment 1: M = 71.1, SD = 9.4; Experiment 3: M = 63.8, SD = 11.0) vs. post-congruent (Experiment 1: M = 69.3, SD = 8.9; Experiment 3: M = 62.4, SD = 11.6) trials in either experiment (Experiment 1, |t| = 1.33, p>.05, Experiment 3, |t| = .85, p>.05).

A second class of alternative interpretation relies not on congruency but on processing time. Specifically, because post-error trials were significantly slower than post-correct trials, it is possible that it was merely the added time spent viewing the objects that drove the improved target memory in post-error trials. To evaluate this possibility, we selected the slowest quartile of post-correct trials to match the RTs of the post-error trials. A paired sample t-test confirmed that the mean RTs between post-error (Experiment 1: M = 700.1, SD = 140.7; Experiment 3: M = 702.1, SD = 87.3) and the slowest quartile of post-correct (Experiment 1: M = 704.7, SD = 146.5; Experiment 3: M = 708.4, SD

= 96.1) trials were not significantly different for either Experiment 1, |t| = .31, p>.05 or Experiment 3, |t| = .43, p>.05. To assess differences in memory for the target objects between post-error and the slowest post-correct trials, hit rate data from each experiment were submitted to a paired sample t-test. For Experiment 1, we observed better memory for the post-error (M = 76.7, SD = 11.4) compared to the slowest post-correct trials (M = 67.1, SD = 9.2), |t| = 4.14, p<.001. Similarly, in Experiment 3, subjects had better memory for the targets presented on post-error (M = 72.8, SD = 12.1) trials than the slowest subset of post-correct (M = 64.6, SD = 10.9), |t| = 2.86, p<.01.

Taken together, these control analyses rule out alternative explanations for the PETE effect based on stimulus congruency and viewing time. In turn, this strengthens the case for the proposition that making an error as such results in time-dependent adaptive refocusing on task-relevant information. Finally, to test the generality of this novel effect, we replicated Experiment 1 but using a prime-probe design (where the distracter is presented in the same location as the target but precedes the target in time) instead of a flanker task design. As reported in Appendix A, in Experiment 4 we again observed a target-selective encoding benefit for post-error trials.

5.7 General discussion

To account for a long history of inconsistent findings and proposals (adaptive vs. maladaptive) on the nature of post-error processing adjustments, Wessel (2018) proposed a time-dependent cascade of error-triggered processes (see also Jentzsch &

Dudschig, 2009) that posits an initial global inhibition of processing, followed by orienting to the error source and a subsequent retuning of attention to the task at hand (to prevent future errors). In the present study, we tested this proposal with a novel approach: a flanker task that employed trial-unique target and distracter stimuli, followed by a surprise recognition memory test. This allowed us to measure the selectivity of post-error stimulus encoding at the single trial level. We combined this novel paradigm with a systematic RSI manipulation to characterize the time-course of the post-error processing cascade. Our results were clear-cut: first, the flanker task showed classic flanker and PES effects across all three experiments, with PERI observed at medium and long RSIs. Second, critically, we observed a reliable, post-error target enhancement (PETE), as reflected in incidental memory, that interacted with RSI. In line with the adaptive orienting theory, post-error targets – relative to flankers – were better remembered than post-correct targets, but this effect was time-dependent; at the short RSI (300ms), post-error stimuli were not encoded any better than post-correct ones, but a target encoding benefit emerged at the medium RSI (650ms), and grew more pronounced at the long RSI (~1000ms). Moreover, these effects were mirrored by trial-specific differences in memory confidence ratings between the target and distracter stimuli. Together, this novel finding suggests that making an error results in enhanced selective task stimulus processing, but that this adaptive process only emerges following an initial period of disrupted task processing.

Despite the improved memory for target stimuli following an error in both Experiments 1 and 3, we only observed PIA in Experiment 1, suggesting that this effect may also be time-dependent. As pointed out in the introduction – the finding of PIA is far from universal in the literature (Moran et al., 2015; van den Brink et al., 2014)(Fiehler et al., 2005; Ullsperger & Szymanowski, 2004), so the boundary conditions for observing PIA represent an interesting question for future research.

As noted in the introduction, Wessel's (2018) proposal integrates a range of superficially inconsistent findings on post-error processing by assuming a time-dependent transition of processing that initially takes focus away from the ongoing task, before being strategically reengaged. We here not only tested this basic idea by assessing post-error behavior over a range of RSIs, but – importantly – we did so by innovating on the traditional behavioral measures of post-error processing (PES, PIA, PERI), all of which have considerable limitations in terms of their sensitivity for measuring cognition and their selectivity to post-error processes. Arguably the most serious drawback of these measures is the fact that they represent aggregate metrics that compare mean RT or accuracy rates between groups of trials, such that they do not allow one to make inferences about how post-error stimuli are processed on any one particular trial. By contrast, the task protocol we validated here grants a lens onto the selectivity of target/flanker encoding on a trial-by-trial basis, as the encoding strength (as gauged by memory confidence) can be compared between targets and distracters for any given trial. This is an advantage even over typical neural measures of post-error processing, like fMRI or EEG, which also rely on averaging activity over many trials (Driel et al., 2012; Iannaccone et al., 2015; Klein et al., 2013).

Given that PETE represents a novel phenomenon, we took a number of steps to ensure the robustness and specificity of this effect. First, we replicated the effect at two RSIs (650 and ~1000ms) and in two protocols, one being the flanker task (Experiments 1 and 3), and the other being a prime-probe task (Experiment 4). Second, we conducted a series of control analyses to rule out that post-error encoding benefits may in fact not be a specific consequence of errors. One alternative explanation for these findings could be that the improvements in memory are the result of differences in congruency rates between post-error and post-correct trials. To address this possibility, we compared the rates of incongruent stimuli between post-error and post-correct trials and found no significant differences. However, since the majority of errors are typically committed on incongruent trials, an additional explanation for the observed findings could be that the adaptive processes are a response to conflict and not errors (Van der Borght et al., 2014). To account for this possibility, we compared target memory for post-incongruent vs post-congruent trials, and found no significant differences. Finally, since the RTs for the post-error trials were significantly longer, the improved memory could be due to prolonged exposure to the stimuli in comparison with the post-correct trials. To test this alternative hypothesis, we compared target memory between post-error trials and the slowest quartile of post-correct trials and again observed target-specific memory improvements for the post-error trials only. Altogether, these control analyses provide strong support for the notion that post-error target encoding benefits are in fact a phenomenon that is specific to error processing.

In contrast to the current findings, a recent study by (Decker et al., 2020) found evidence for impaired memory for target stimuli following an error across two experiments. However, there are two major differences between the experimental designs that could explain this disparity. First, it is likely that the cause of an error affects the manner in which cognitive processing is adapted in response to that error (Driel et al., 2012). It is well-established that the conflict in information processing that gives rise to errors can stem from different sources (Kornblum et al., 1990), and that different sources of conflict are adapted to via distinct mechanisms (for reviews, see Braem et al., 2014; Egner, 2008). Namely, conflict stemming from clashing semantic stimulus representations appears to be resolved by attentional biasing of stimulus processing (re-focusing on target stimuli; e.g., Egner & Hirsch, 2005), whereas conflict arising at the level of response selection appears to be adapted to via biased motor processing (Egner et al., 2007; Forstmann et al., 2008).

We posit that in Decker et al.'s (2020) experiments, errors are fostered by conflict at the response level, whereas in our experiments errors arise from conflict between semantic stimulus properties. In particular, Decker and colleagues' first experiment employed a categorization task in which 90% of images belonged to a frequent category and 10% to an infrequent category; errors in this set-up are thus induced by creating a pre-potent response bias. Similarly, their second experiment used a Simon task, which is considered a canonical example of response conflict (e.g., Kornblum et al., 1990; Ridderinkhof, 2002). Specifically, participants categorized images as natural or man-made using left and right-hand buttons, and images were presented either to the left of right of fixation. Here, errors occur due to (spatial) conflict in response selection on incongruent trials, where the position of the stimulus is incompatible with the location of the correct response button. Given that errors in the study by Decker et al. (2020) were likely due to response conflict, one would not expect adaptation to these errors to be focused on stimulus processing (Egner, 2008), and thus it is not surprising that memory for post-error stimuli was impaired (for similar findings in response inhibition tasks, see Chiu & Egner, 2015). By contrast, in the present experiments, errors arise from the clashing of semantically incompatible stimulus categories, which is precisely the scenario where one would expect to observe stimulus-focused adaptation in the shape of enhanced attention to target stimuli (Egner & Hirsch, 2005).

The second major difference between the tasks is the presence of the stimuli after participants have made a response. Our results suggest that the length of the RSI influences post-error processing because it alters that amount of time available to go through the cascade of post-error processes outlined by Wessel (2018). In our task, the fixation cross is the only object that appears on the screen during this period. However, in Decker at al.'s paradigm, the stimulus remains on the screen for 1000 ms followed by a 500 ms inter-trial interval (ITI), regardless of the response time. The presence of the stimulus during post-error processing may alter the amount of time spent in each stage of the post-error processing cascade, potentially increasing the amount of time needed to reach the adaptive processing stage. Follow-up neuroimaging studies are needed to further investigate both the amount of time spent in each step of post-error processing cascade and the different factors that may modify that time.

There are a variety of potential interesting avenues for applying the current approach to further probe post-error cognition. First, an obvious extension of interest would be to cover a wider and/or finer distribution of RSIs, to obtain a higher-resolution picture of the post-error processing cascade. For example, while the shortest RSI in the present study (300ms) showed no advantage for post-error encoding, both post-error and post-correct targets were in fact remembered at above chance levels by most participants. This finding seems to be at odds with the assumption of a global inhibition of cognitive processing in response to the (surprising) error event (Wessel, 2018), but it is of course possible that target encoding would drop to chance at an even shorter RSI, and this could be probed in a future study. Similarly, the present study shows that adaptive effects are absent at 300ms but already reliable at an RSI of 650ms; a more fine-grained RSI manipulation could resolve the exact time-point at which the encoding benefits emerge, and thus detail more precisely the duration that the hypothesized initial inhibition and error-orienting may take.

Second, Wessel (2018) suggests that while the initial inhibition of ongoing activity and attentional orienting to the error source are automatic, the subsequent adaptive control processes are deliberate, which suggests that the latter should be malleable by contextual factors. The present protocol could also be adapted to test this notion. For instance, in the present study, RSIs remained constant throughout each experiment; this presumably resulted in participants being aware of roughly how much time they have before the next trial to implement control processes following an error, which may affect their willingness (in addition to their ability) to do so. The present approach could be modified by intermixing RSIs in a single experiment, so that participants cannot anticipate the amount of time they will have for post-error processing; assuming that the adaptive adjustments are in fact strategic, participants should be more reluctant to engage post-error control in this scenario (in line with the notion of control being engaged based on its expected utility; Shenhav et al., 2013). As a further extension of the current work, one could also employ electroencephalography to gain further insights into the neural time-course of post-error processing and the underlying neural mechanisms, by adjusting the RSIs according to the timing of the cascade of processes as reflected by event-related potentials. Additionally, future studies using eye-tracking could further investigate the attentional orienting response to explore differences based on the type of error committed (i.e., due to distraction vs failure to inhibit a motor response) on a trial-by-trial level and determine whether those differences are predictive of the type of control mechanism implemented and its influence on subsequent memory.

In conclusion, we evaluated post-error cognition, and specifically the adaptive orienting theory (Wessel, 2018), with a novel task combining trial-unique targets and distracters with a surprise recognition memory test that allowed us to probe the attentional selectivity of post-error stimulus processing on a trial-by-trial basis. By combining this approach with a systematic manipulation of RSIs, we mapped out the time-course of post-error stimulus encoding. We demonstrated a novel effect: a time-dependent post-error enhancement of (selective) target stimulus encoding (PETE). In line with the adaptive orienting theory, this effect was absent at a short RSI, emerged at intermediate RSI duration, and grew larger at a yet longer RSI. Our novel approach represents a promising new tool for further elucidating the exact nature and time-course of post-error cognition.

6. Conclusions

6.1 Study summaries and future directions

In Study 1, using electroencephalography (EEG), I investigated the attentional processes underlying the formation and encoding of self-generated mental images into episodic memory. Participants viewed flickering words referring to common objects and were tasked with forming visual mental images of the objects and rating their vividness. Subsequent memory for the presented object words was assessed using an old-new recognition task. Internally-directed attention during image generation was indexed as a reduction in steady-state visual evoked potentials (SSVEPs), oscillatory EEG responses at the frequency of a flickering stimulus. The results yielded three main findings. First, SSVEP power driven by the flickering word stimuli decreased as subjects directed attention internally to form the corresponding mental image. Second, SSVEP power returned to pre-imagery baseline more slowly for low- than high-vividness later remembered items, suggesting that longer internally-directed attention is required to generate subsequently remembered low-vividness images. Finally, the event-related-potential (ERP) difference due to memory (Dm) was more sustained for subsequently remembered low- versus high-vividness items, suggesting that additional conceptual processing may have been needed to remember the low-vividness visual images. Taken together, the results clarify the neural mechanisms supporting the encoding of self-generated information.

In Study 2, again using EEG, I examined the neural processes associated with the retrieval of previously generated visual mental images, focusing on how the vividness at generation can modulate retrieval processes. Participants viewed a series of word stimuli referring to common objects, forming a visual mental image of each word and rating its vividness. This was followed by a surprise old/new recognition task to assess subjects' memory for the objects. I compared performance at retrieval for items that had been rated as high- versus low-vividness at encoding. High-vividness items were retrieved with faster reaction times and higher confidence ratings in the memory judgment. While controlling for confidence, neural measures of brain activity indicated that high-vividness items produced an earlier decrease in alpha-band activity at retrieval compared to low-vividness items, suggesting an earlier memory reinstatement. Even when low-vividness items were remembered with high confidence, they were not retrieved as quickly as the items that had been encoded with high-vividness.

In Study 3, I investigated the interactions between sustained attention (SA) and memory, thereby broadening my research, which had previously focused on selective attention. SA refers to the ability to maintain cognitive focus on a task over an extended period of time. SA fluctuates over time, and failures of SA can occur in various ways. For example, while listening to a lecture, our attention may be diverted to the movement of a nearby person (external distractor) or to random thoughts (internal distractor). Using a combination of fMRI and pupillometry, I investigated SA fluctuations and their influence on subsequent memory. A series of object images were presented, each in front of a background image of a face or house. Participants were instructed to ignore the background image and attend only to the objects, responding with one button press on 90% of trials, and an alternate button for toy-object images (10% of trials). In a subsequent forced-choice recognition phase, each seen object was paired with a new object of the same name, and participants selected the seen object while rating their confidence. Subsequent memory analyses yielded reduced activity in parahippocampal place area (PPA), fusiform face area (FFA), and retrosplenial cortex (RSC), suggesting that suppressing attention to irrelevant objects/houses and unrelated thoughts (default mode network—DMN) improved subsequent memory. Later remembered items were also associated with increased activity in the lateral occipital complex (LOC) and slower RTs, likely reflecting greater encoding processing, as well as larger pupil size, which has been previously associated with SA. Taken together, these results clarify the neural mechanisms of SA and suppression of external and internal distractions, as well as the impact on episodic encoding.

In Study 4, I extended my research to investigate the interactions between cognitive control and memory. More specifically, I investigating the attentional adjustments that occur following the commission of an error and their influence on subsequent memory. To do this, I devised a novel object flanker task that employed trial-unique target and distracter stimuli and was followed by a surprise recognition memory test. This allowed me to determine how errors influence incidental target and distracter encoding in a trial-specific manner. I used this approach to test the “adaptive orienting theory” of post-error processing, according to which an error triggers an initial inhibition of task processing - facilitating orienting to the error source - followed by a controlled re-tuning of attention to the task. To characterize the time-course of the post-error processing cascade, I combined the task with a manipulation of the response-stimulus interval (RSI), across four experiments (RSIs: 300ms, 650ms, ~1000ms; N = 96-100 per experiment). Results showed that making an error leads to a substantial (~10%) enhancement of target (but not distracter) memory on the subsequent trial, which interacts with RSI: post-error targets were remembered better than post-correct targets at the long (650ms, ~1000ms) but not the short (300ms) RSIs. These findings provide clear support for the adaptive orienting theory by demonstrating a novel cognitive phenomenon: a time-dependent post-error enhancement of target encoding (PETE).

6.2 Future directions

In Study 1, I demonstrated a novel use of steady-state visual evoked potentials (SSVEPs) as an index of internally-directed attention. Future research is needed to validate this method and better understand the nuances and limitations. For example, the results showed a decrease in SSVEP power when participants directed their attention internally to form the visual mental images. It would be interesting to investigate whether the magnitude of the dip would vary for different types of internally-directed attention tasks that would require various levels of focus. Additionally, future studies could use SSVEPs to track shifts between internally- and externally-directed attention as participants are performing a more complex paradigm. The second main finding in this study was that the difference due to memory (Dm) effect was more sustained for the subsequently remembered low-vividness items compared to high-vividness. This could be because additional conceptual processing was needed in order to successfully encode the low-vividness items. Further research is needed to directly test this interpretation. Future studies directly comparing different encoding strategies would give more insight into the causes of a change in the duration of the Dm.

In Study 2, I investigated the neural mechanisms underlying the retrieval of visual mental images and found an earlier latency decrease in alpha power for items that had been rated as high-vividness at encoding. To extend these findings, future studies could directly compare the retrieval of visual mental images to images that had been visually presented. Additionally, an MRI study would give further insights into the brain regions involved. It would be interesting to compare the reinstated representations to see if there are differences in the fidelity of the retrieved information.

In Study 3, the findings were confined to specific regions of interest that have been shown to be modulated by attention for the relevant stimuli that were present. Further analyses are needed to delineate the neural underpinnings of external distraction vs mind-wandering during SA. Studies have shown at least three different brain networks involved in SA: the dorsal attention network (DAN), the default mode network (DMN), and the frontoparietal control network (FPN). The DAN and the DMN have been associated with external and internal attention, respectively, while the FPN is associated with cognitive control. A direct comparison of the failures of SA that are due to external distraction vs. mind-wandering would further clarify the roles of each network in the fluctuations of SA and their unique influence on subsequent memory.

In Study 4, I observed a target-specific and time-dependent post-error memory enhancement that can be explained by an adaptive control mechanism initiated following the commission of an error. An EEG study with the current paradigm would give insights into the neural mechanisms that are initiated following an error as the response-stimulus interval is manipulated. If the adaptive orienting theory is correct, the results would show a cascade of neural processes that is interrupted when the response-stimulus interval is too short. There could also be various consequences to interruptions occurring at different time-points.

6.3 Conclusion

Taken together, these four studies offer a more nuanced look into the interactions between attention, cognitive control, and memory. A lot of time has been spent on selective, externally-directed attention. However, attention can be directed externally or internally, it can be selective or sustained, and it can be goal-directed or spontaneous. When we are processing information, we could be switching between any one of these types of attention with varied mnemonic consequences. Therefore, moving toward more and more intersectional research relying on a variety of methodology can offer us the most comprehensive answers to our questions.

Appendix A

A.1 Experiment 4: Prime-probe task

To test the generalizability of our findings to other interference tasks, we designed a prime-probe task with parameters closely matched to Experiment 1 (see **Figure 21**). We expected similar post-error improvements in memory specific to the probe, which would indicate that post-error target encoding benefits do not depend on the particulars of the flanker task employed in Experiments 1 and 3.

A.1.1 Methods

A.1.1.1 Participants

The recruitment target and procedure were identical to Experiment 1. 108 participants from MTurk provided informed consent in accordance with Duke University's Institutional Review Board (mean age = 34.13, SD = 8.63; 43 female). Participants were excluded if their error rate was less than 10% (N=5), if over 30% of error occurred as multiples in a row (N=2), or if memory was at chance (N=2). The final sample size was 100.

A.1.1.2 Stimuli and procedure

Participants were presented with an object image prime followed by an object image probe. The object images used were the same as Experiments 1-3 and were presented in color at 85×85 pixels. Participants were instructed to categorize the probe image on each trial. To match the parameters of Experiment 1, the task included 120 trials, each lasting a total of 1600ms. On each trial, the prime was presented for 600ms followed by the probe for 600s, with an ITI of 400ms. After completing the task, participants filled out a demographic questionnaire, followed by a surprise memory test. As in the previous experiments, participants were presented with the 240 images they had previously seen, randomly intermixed with 120 new images for a total of 360 trials. Once again, images were presented one at a time for up to 3 seconds or until a response was recorded. Participants categorized each image as old or new and rated their confidence from 1 (definitely new) to 6 (definitely old) using the keyboard number pad.

A.1.1.3 Analyses

The analyses were the same as in Experiments 1-3.

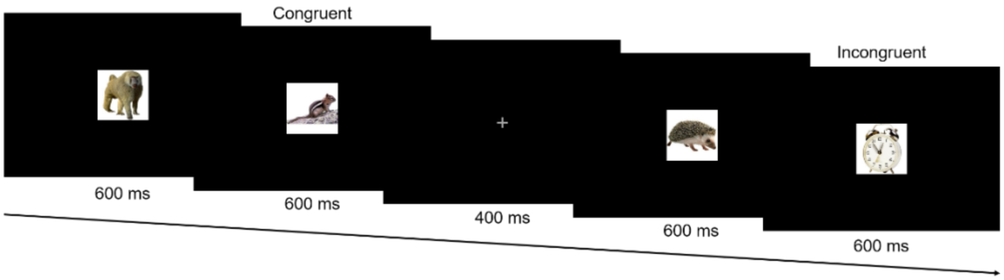

Figure 21: Prime-probe task paradigm. Each trial began with the presentation of an object image prime presented for 600ms, followed by a congruent or incongruent object image probe presented for 600ms, with an ITI of 400ms. Subjects were instructed to categorize the probe image as living or non-living.

A.1.2 Results

A.1.2.1 Prime-probe task

The overall error rate was 24.8%, with the greater proportion of errors stemming from incongruent (M = 14.0, SD = 4.2) compared to congruent trials (M = 10.9, SD = 3.2),

|t| = 5.82, p<.001. **Table 11** displays means and standard deviations for the RT data. As in Experiments 1-3, RT data were submitted to a 2 (congruency: congruent vs. incongruent) × 2 (trial type: post-correct vs post-error) rANOVA. There was a main effect of congruency, F(1,99) = 274.45, p<.001, with slower RTs for incongruent (M = 550, SD = 53) compared to congruent (M = 533, SD = 40) trials. Additionally, there was a main effect of trial type. Significant RT slowing was observed for post-error (M = 578, SD = 56) compared to post-correct (M = 532, SD = 45) trials, F(1,99) = 24.46, p<.05. Unlike in Experiment 1, there was no interaction between congruency × trial type, F(1,99) = 2.11, p>.05.

A.1.2.2 Incidental memory

Table 12 displays means and standard deviations for the memory data. The hit rate was 67.3%, and the false alarm rate was 24.0%, indicating that memory performance was well above chance, |t| = 5.34, p<.001. As in Experiments 1-3, data were submitted to a 2 (trial type: post-correct vs. post-error) × 2 (stimulus feature: cue vs. probe) rANOVA. There was a main effect of trial type, as stimuli from post-error (M = 71.0, SD = 11.1) trials were better remembered than those from post-correct (M = 64.3, SD = 9.9) trials, F(1,99) = 6.92, p<.01. There was a main effect of stimulus feature, as well, with better memory observed for the probes (M = 72.4, SD = 9.9) than the primes (M = 62.1, SD = 10.9), F(1,99) = 253.78, p<.001. Crucially, akin to Experiments 1 and 3, these effects were qualified by an interaction between trial type and stimulus feature, F(1,99) = 6.26, p<.02.

Post hoc Bonferroni-corrected pairwise comparisons indicated significantly improved post-error compared to post-correct memory for the probes ($|t| = 3.14$, $p<.05$), but not for the primes ($|t| = .84$, $p>.05$).

A.1.3 Discussion

Similar to the results of Experiment 1, we replicated typical congruency and post-error effects reported in previous studies. Additionally, we replicated the post-error improvements in memory observed in Experiments 1 and 3, and these memory improvements were selective for the probes, just as they were for the targets in the flanker task. These results document that the post-error target enhancement (PETE) observed in the flanker task generalizes to a prime-probe task, and is thus not dependent on the particulars of the flanker task design.

Table 11: Means and standard deviations for response times (ms) during prime-probe task.

	Post-Correct	**Post-Error**
Congruent	525 (38)	575 (42)
Incongruent	539 (49)	581 (57)

Table 12: Means and standard deviations for percent of stimuli remembered as a function of error.

	Post-Correct	**Post-Error**
Probe	68.2% (9.7)	77.9% (10.8)
Prime	60.4% (10.0)	64.1% (11.2)

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Biography

Eva Gjorgieva was born on April 11, 1993 in Stip, Macedonia. She received her B.S. in Psychology from Loyola University Chicago in 2015, where she graduated *cum laude,* with distinction, and with a minor in Neuroscience. While at Loyola, Eva received the Provost Research Fellowship and the Mulcahy Research Scholarship in support of her undergraduate research, which was supervised by Dr. Rebecca L. Silton. She also served as the Vice President of Psi Chi and received a Psi Chi Research Grant from the American Psychological Society. Eva then spent two years as a research technician for Dr. Jay Gottfried at Northwestern University.

In 2017, Eva enrolled as a graduate student at Duke University through the Cognitive Neuroscience Admitting Program. She joined the labs of Dr. Marty Woldorff, Dr. Roberto Cabeza, and Dr. Tobias Egner in the Department of Psychology & Neuroscience, earning an M.A. in 2020. Eva's doctoral research has been published in *The Journal of Experimental Psychology: General* and *Cerebral Cortex.* Her research was supported by a Ruth L. Kirchstein National Research Service Award Individual Predoctoral Fellowship, as well as two Charles Lafitte Foundation Program Grant Awards. Eva also received a National Science Foundation Graduate Research Fellowship Honorable Mention.