Behavioral and Neural Mechanisms Underlying the Differential Effects of Location and Object Overlap on Learning and Memory

by

Benjamin Joseph Chaloupka

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Dissertation Committee:

Dr. Dasa Zeithamova, Chair

Dr. Ben Hutchinson, Core Member

Dr. Brice Kuhl, Core Member

Dr. Graham Kribs, Institutional Representative

University of Oregon

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DISSERTATION ABSTRACT

Benjamin Joseph Chaloupka

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We often have new experiences that overlap with our prior experiences in some way. In some cases, this leads to facilitation of new learning, while it causes interference in others. While both of these effects are the result of overlapping experiences, research on facilitation and interference have largely remained separate. Thus, a unified investigation is necessary to identify conditions of overlap that differentially cause facilitation and interference.

Across three studies, this dissertation explores how the type of overlap can differentially affect learning and memory, and how the brain differentially supports learning depending on the type of overlap. Chapter II introduces a novel object-location paired-associates grid task designed to investigate both facilitation and interference simultaneously. In two experiments, we found that overlapping locations caused facilitation of new learning while overlapping objects caused interference. Chapter III aims to replicate these findings using a different version of the grid task. We found partial evidence that both effects generalize to different response procedures. Chapter IV utilizes fMRI to examine how the brain supports learning under different overlap conditions. We found that location similarity in vmPFC was positively related to facilitation. We also found increased activation in PHC during the location overlap condition. Collectively, these findings demonstrate that the type of overlap determines its effect on learning and memory and elucidates how the brain differentially supports learning under different conditions of overlap.

This dissertation includes previously published co-authored material.

CURRICULUM VITAE

NAME OF AUTHOR: Benjamin Joseph Chaloupka

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
University of Illinois at Chicago, Chicago
Elgin Community College, Elgin

DEGREES AWARDED:

Doctor of Philosophy, Psychology, 2025, University of Oregon
Master of Science, Psychology, 2020, University of Oregon
Bachelor of Arts, Psychology, 2018, University of Illinois at Chicago
Associate of Arts, Psychology, 2016, Elgin Community College

AREAS OF SPECIAL INTEREST:

Cognitive Neuroscience

PROFESSIONAL EXPERIENCE:

Graduate Employee, University of Oregon
September 2019 – June 2025

Content Engineer, Oregon Research Institute
July 2020 – July 2022

Research Assistant, UIC Memory Lab
September 2017 – May 2019

GRANTS, AWARDS, AND HONORS:

Distinguished Teaching Award, University of Oregon, 2024

Kimble First-Year Teaching Award, University of Oregon, 2022

Division of Graduate Studies University Award, University of Oregon, 2021

Summa Cum Laude & Departmental Distinction, University of Illinois at Chicago, 2018

Graduated with Honors, Elgin Community College, 2016

PUBLICATIONS:

Murray, A. & **Chaloupka, B.** (2025). Transitive inference as an intrinsic process. *Oregon Undergraduate Research Journal, 23*(1), 1-7.

Chaloupka, B. & Zeithamova, D. (2024). Differential effects of location and object overlap on new learning. *Frontiers in Cognition, 2*. https://doi.org/10.3389/fcogn.2023.1325246

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DEDICATION

I dedicate this dissertation to Mother Earth, my greatest teacher, whose mountains, forests, and raw beauty inspire me in every part of my life.

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CHAPTER I

INTRODUCTION

The field of cognitive psychology is in its infancy relative to many other sciences. Despite this, the past century has yielded a rich body of work studying learning and memory. Perhaps this is no surprise, given that our memories allow us to navigate the world and to have a sense of self. Thus, memory was one of the first aspects of cognition to be examined, and it still stands center stage in the modern world of cognitive neuroscience. For all of our collective inquiry, theory, and experimentation, there is still much that lies beyond our current understanding. We still ask why we remember some things and forget others, why common threads of experience facilitate learning in some instances but interfere with learning in others, and which brain regions or networks are responsible for these things and how. Here we will explore some of the research that has attempted to answer these questions and has led to the central research question of this dissertation: why do overlapping experiences facilitate new learning in some cases but hinder learning in others?

Facilitation and Schemas

Frequently, we rely on our collective past experiences to navigate new events. Our past experiences facilitate new learning. For example, imagine that you have gone to your favorite conference every year that is always in the same city at the same venue. It only took a couple times for you to learn the layout of the venue. Now, you know where the poster sessions will be, which rooms will host the symposia, and the location of the smaller rooms that would host the data blitz talks. One year, another conference that you typically attend holds its annual meeting at that very same venue. Despite the format of this conference being quite different, you quickly learn the location of each piece of the conference within the venue. In this example, you have

developed a framework based on your past experiences. This new experience overlaps with this framework, allowing for rapid learning of the other conference's layout within the venue.

Facilitation of new learning has long been studied in the form of schemas, a concept first formalized by F. C. Bartlett (1932). While Bartlett himself did not like the word 'schema', he admitted that he did not have a better alternative, so he provided the earliest formal definition of a schema as so far as how the term is used today: "'Schema' refers to an active organisation of past reactions, or of past experiences, which must always be supposed to be operating in any well-adapted organic response," (Bartlett, 1932, p. 201). This definition successfully captures the essence of a schema. First, he describes the active organization of past experiences. A schema is formed when overlapping experiences are integrated into a concept, category, or other generalized form of knowledge. The second half of the definition indicates that schemas are inherently facilitatory in their nature. We form these generalizations to provide us shortcuts – adaptive ways to increase efficiency while navigating the world. By fitting our new experiences into established mental frameworks, we can learn new information more quickly.

In an early study, Attneave (1957) claimed to be the first to experimentally test whether learning a schema would facilitate subsequent learning. He conducted two experiments, one with letter-pattern schemas and the second with polygon schemas. In the first, three prototypes of letter-patterns were created along with eight variants of each prototype. In the second, five 6-sided and five 12-sided polygon prototypes were constructed, along with two sets of eight variants from each prototype. In both experiments, participants who were pretrained on the schema prototypes committed fewer errors than control participants on a paired-associates task with the variants. He interpreted his results as a demonstration that schemas are highly important for learning. A prototype can represent the central tendency of a schema, such as the geometric

schemas used in this study. Thus, learning a prototype can facilitate learning of related items. In an adjacent line of work, Posner and colleagues (1967) found that the learning rate of geometric patterns was directly related to their level of distortion. The more similar a pattern was to a prototype, the more quickly it was learned.

In the decades following this early work, schemas have been studied at length. In one study, biology and education students were recruited as participants. In a first session they learned new facts, some of which were related to biology and some to education. During a retrieval session the following day, participants performed significantly better on facts that were related to their program in school than on those that weren't (van Kesteren et al., 2014). This example shows that a well-established schema – the framework of an academic field – strongly facilitates learning of new, related information. The study of schemas has extended beyond semantic schemas to many other contexts and modalities. For example, King and colleagues (2019) used a motor sequence task to demonstrate that motor learning is facilitated via integration with a previously learned schema.

Spatial Schemas

One schema type of particular interest is the spatial schema. In a seminal paper, Tse and colleagues (2007) provided compelling evidence for the instantiation of spatial schemas in rats using a flavor-place paired-associates task. Over several sessions, the rats were trained to learn a spatial schema consisting of flavor cues placed in sand wells in an arena. After learning the schema, two of the flavor cues were replaced by new targets and moved to adjacent locations. The rats were able to learn these new traces in only a single trial by integrating them with, or updating, their existing spatial schema. This was the first direct evidence of a spatial schema facilitating new learning.

This work inspired further investigation of spatial schemas, and they have since been studied in humans. In one study, van Buuren and colleagues (2014) demonstrated that a similar associative spatial schema facilitated new learning in humans. In another study, an analogous spatial schema task confirmed these results, showing a clear facilitation effect both during training and later test (Guo & Yang, 2020). To further solidify these findings, Kyle and colleagues (2015) utilized a novel task design in which participants learned spatial schemas via city layouts in a virtual environment. They found that participants performed better in the retrieval phase for cities with similar spatial layouts as the previously learned city than for cities with entirely new spatial layouts, demonstrating that the benefit of spatial schemas is not limited to a grid-like associative schema.

Additional evidence for spatial information's unique role in memory organization lies outside the context of schemas. In one example, researchers found that increased familiarity with a specific location led to increased vividness of imagined future events across three experiments (Arnold et al., 2011). First, they found that the increased vividness of imagined events in the near future compared to distant future events was driven by clarity of location. Additionally, they found that near future events were more likely to be imagined in familiar locations. Finally, they found that future events in familiar locations are imagined more clearly than events in unfamiliar locations. Collectively, these experiments demonstrate the central role of spatial information in our ability to clearly imagine future events. In another study, participants read scenarios with either a person or location as a context cue and later had to recall details about the scenario (Robin et al., 2016). Not only were locations a more effective context clue than people, but participants in the person context condition were very likely to spontaneously generate location details while participants in the location context condition were far less likely to come up with

person details. Their findings demonstrate that spatial information provides a scaffold for episodic memory, playing a central role in one's ability to remember specific events.

Others have recognized the unique advantages of spatial information and leveraged them into memory strategies. The 'method of loci', an ancient memory system employed by the Greeks and Romans, was revived by Ross and Lawrence (1968). This strategy involves selecting 'loci', such as rooms or other features, within a house or familiar building, and placing memory targets, such as objects or words, in those locations. By imagining walking through this building from one location to the next, one can encode these memories by visualizing a representation of one target per location and later retrieve them with a similar imaginary walk. Employing this strategy drastically improved the memory performance of participants on both a serial learning task and a paired-associates task (Ross & Lawrence, 1968). In a later study, researchers found that the method of loci led to improved memory performance after a 2-day delay compared to other memory strategies (Wang & Thomas, 2000). Collectively, these results suggest that spatial information holds an important role in learning and memory.

Schema Acquisition Timeline

It has long been believed that schemas take a relatively long time to develop. In one study, Sommer (2016) demonstrated that learning of novel semantic information was improved by anchoring it to existing schemas using a longitudinal 302 day study. Similarly, in Tse and colleagues' seminal paper (2007), the rats learned the spatial schema over the course of many sessions spanning several months.

However, recent evidence suggests that schemas may form more quickly than we originally thought. A study by Tompary and colleagues (2020) leveraged a creative experimental design to demonstrate that schema learning occurs in conjunction with episodic learning.

However, we tend to rely on our more detailed episodic memories in the short run, and we shift towards schema memory as our episodic memories weaken over time. Thus, schemas may form quite quickly but are not fully utilized until our more transient episodic memories fade. This finding sheds some light on the acquisition timeline for schemas.

Neural Correlates of Schemas

While research on schemas and facilitation has been around for nearly a century, the advent of neuroimaging technology came after schema research had taken a back seat to other inquiries into the workings of learning and memory. However, Tse and colleagues (2007) sparked a resurgence of interest into the topic. Armed with modern neuroimaging tools, researchers began to investigate the neural underpinnings to the formation and instantiation of schemas. In a landmark review paper, van Kesteren and colleagues (2012) proposed a framework entitled SLIMM (schema-linked interactions between medial prefrontal and medial temporal regions). SLIMM posits that neural representations are shifted from the medial temporal lobe (MTL) to neocortex, accelerated by the medial prefrontal cortex (mPFC). Specifically, mPFC aids in the consolidation of new information that fits within an existing schema. While the MTL-neocortex shift was not a novel hypothesis, their formalization of the mPFC's role in schema-related learning was a breakthrough.

Building on this work, Gilboa and Marlatte (2017) published a review in which they found some evidence for SLIMM, but also extended our understanding of schemas in the brain. They highlighted evidence that the relationship between the MTL and the ventromedial prefrontal cortex (vmPFC) is critical to schema-related memory, as proposed by SLIMM. Additionally, they identified the hippocampus as a central piece of the puzzle. They also proposed roles for the anterior temporal lobe (ATL) and posterior cortical regions such as the

retrosplenial cortex (RSC), the temporoparietal junction (TPJ), and the angular gyrus (AG). While they ended their review with several outstanding questions, they honed our understanding of schemas in the brain, focusing on vmPFC-hippocampal-posterior cortical interactions.

Memory Generalization in the Brain

In an adjacent line of work, researchers have investigated the neural underpinnings of memory generalization – the ability to use prior knowledge to make predictions in novel situations. While schemas are one example, memory generalization more broadly includes any situation in which we can rely on our past experiences to make inferences in new but similar scenarios. As with schemas, early neuroscientific investigation into memory generalization discovered a central role for the hippocampus and its interactions with other brain regions.

In one study, integrative encoding in the hippocampus and midbrain was linked to successful memory generalization, where overlapping events are integrated into a unified representation (Shohamy & Wagner, 2008). Using an associative inference task, Zeithamova and Preston (2010) found that activity during encoding in the hippocampus and parahippocampal cortex (PHC) predicted successful generalization, while interactions between prefrontal cortex (PFC) and MTL during retrieval were predictive of success.

One purported neural mechanism for successful memory generalization is memory integration, in which overlapping events evoke more similar, or integrated, patterns of neural activity in specific brain regions. This is often measured via pattern similarity analysis, where voxel-wise patterns of activation within a specific region of interest during one event are correlated with patterns of activation during a second event. The higher the correlation, the more similar the patterns of neural activity are for a given pair of events. There is some evidence that distinct subfields in the hippocampus play different roles in memory. Making use of high-

resolution functional magnetic resonance imaging (fMRI), Schlichting and colleagues (2014) examined the role of hippocampal subfields in memory generalization. They found evidence for the cornu ammonis 1 (CA_1) subfield's role in memory integration, including increased neural pattern similarity between encoding and retrieval during successful generalization. These findings were summarized in a review by Schlichting and Preston (2015), in which they highlight mPFC-hippocampal interactions along with the CA_1 subfield's role in pattern integration. To bring things full circle, the same lab that released the seminal 2007 paper used the insights from human neuroimaging to test for evidence of hippocampal interactions during memory integration in rats (Takeuchi et al., 2022). Sure enough, they found that hippocampal-neocortical interactions supported integration of new memories into existing schemas, with specific emphasis on hippocampal subfields CA_1, CA_3, and dentate gyrus (DG).

While some research focuses on hippocampal subfields, an adjacent line of research proposes a dissociation along the long axis of the hippocampus, such that the anterior hippocampus represents more generalized, coarse-grained information, while the posterior hippocampus represents more specific, fine-grained information. In one such study, researchers found evidence for a dissociation between memory integration and separation, such that memory for individual events is associated with neural patterns in posterior hippocampus, anterior mPFC, and inferior frontal gyrus (IFG), while integrated memories are associated with neural patterns in anterior hippocampus and posterior mPFC (Schlichting et al., 2015). To further corroborate these findings, Robin and Moscovitch (2017) published a review in which they posit that fine-grained memory is supported by the posterior hippocampus, "gist-like" memory by the anterior hippocampus, and schemas by the vmPFC. Bowman and Zeithamova (2018) provide additional evidence for the role of anterior hippocampal interactions with vmPFC in memory generalization

using a category learning task. While the relative impact of hippocampal subfields versus the anterior/posterior split remains an open question, the field has converged on the importance of the hippocampus and its cortical interactions in memory generalization.

Interim Summary

Collectively, this brief overview of past literature reveals three things: 1) new experiences are integrated with overlapping past experiences, often in the form of a schema; 2) overlap of new events with prior experience, via schema or other form of memory generalization, facilitates new learning and enhances memory; and 3) memory generalization, including schemas, is supported by hippocampal-vmPFC interactions, and CA_1 specifically supports generalization via neural pattern integration. While our understanding of schemas and memory generalization has come into focus over the years, there are still many remaining questions. For example, our grasp on the neural underpinnings of these phenomena is still evolving. Additionally, despite substantial evidence for facilitation via overlap of experience, this fails to explain the whole story. Next, we will explore the dark side of overlapping experience.

Memory Interference

Let us return to your favorite conference. One year, the typical venue is undergoing remodeling, so the conference is held at a new venue across town. The layout of the new venue is quite different, and even by the end of the conference you still feel lost trying to find some of the smaller talks. Instead of going downstairs and to the right as in the typical venue, the data blitz rooms are tucked away to the left on the third floor. In this case, your prior experiences at this conference are *interfering* with your ability to learn its new layout at this new venue. Contrary to what we reviewed above, your overlapping experiences are hindering new learning.

The first study to experimentally test interference was conducted by John A. Bergström (1893). He used a card sorting task to identify proactive interference – when previously learned information hinders new learning – as the main cause of forgetting, controlling for cognitive effort. Despite this early discovery, the field of psychology then turned its attention to the study of retroactive interference – when new information hinders the ability to remember previously learned information. Decades later, Maslow (1934) found evidence for both retroactive and proactive interference, suggesting that perhaps both may be a source of forgetting. Continuing this idea, Melton and von Lackum (1941) designed an experiment using lists of 3-consonant syllables to test both retroactive and proactive interference, finding evidence for both. Critically, this was one of the first studies that demonstrated that greater overlap led to greater interference – both retroactive and proactive.

Proactive interference didn't command the interest of researchers on its own until a seminal paper was published by Benton J. Underwood (1957). In this review, Underwood convincingly argues that proactive interference is the primary source of forgetting in several classical experiments. Additionally, he notes that similarity – both of stimuli and of context – is the central factor at play. A few years later, he followed this by collaborating on an experimental paper in which they demonstrated that proactive interference affects short-term and long-term memory similarly (Keppel & Underwood, 1962).

Another study demonstrated that proactive interference is a function of stimulus similarity using both consonant strings and number strings (Wickens et al., 1963). Proactive interference persisted when the stimuli were of a similar type but was mitigated when the stimulus type changed. Additionally, contextual similarity leads to greater proactive interference:

changing the testing environment for participants mitigated interference effects (Dallet & Wilcox, 1968).

In the decades following this early work, the relationship between similarity and proactive interference has been expanded to many domains. In one study, proactive interference was observed in bilingual participants while word lists were in the same language, but interference was mitigated when the language of subsequent word lists changed (Goggin & Wickens, 1971). In another, proactive interference was observed when lists contained words of a common semantic category, but was mitigated when the semantic category changed between lists (Wixted & Rohrer, 1993). Yet another found evidence for proactive interference driven by stimulus similarity in both an operation span task and a probed recall task (Bunting, 2006). Collectively, these studies provide myriad examples of the effects of proactive interference, as well as the relationship between similarity and interference.

Interference in Associative Memory

In their review, Kliegl and Bäuml (2021) summarize the effects of proactive interference across three kinds of experimental tasks: paired-associates learning, the Brown-Peterson task, and multiple-list learning. In this chapter, the evidence reviewed thus far has come primarily from studies employing one of the latter two task types, both of which require participants to learn lists of individual items. However, there is also early evidence for the effects of proactive interference on associative learning.

The classic AB/AC task is a commonly employed paired-associates learning paradigm. In this task, participants learn one set of paired-associates (AB), and then a second set of either overlapping (AC) associations or non-overlapping (DE) associations. In the 70's, two parallel studies found that participants had greater difficulty learning the AC associations than the DE

associations due to proactive interference from the original AB associations (Postman et al., 1974; Tulving & Watkins, 1974). In other words, when participants learned that one stimulus (A) was associated with another stimulus (B), it was challenging to learn the association of a third novel stimulus (C) with the original (A).

Neural Pattern Separation

The advancement of neuroimaging technology has yielded new questions in the field of memory interference. One critical question is how the brain resolves interference between competing stimuli. One theory that emerged posits that our neural representations of highly similar stimuli actually become more distinct, leading to better memory of overlapping experiences. Early evidence for neural pattern separation was found using rodents, identifying the hippocampal subfields CA_3 and DG as key brain regions (Leutgeb et al., 2007). These findings were extended to the human hippocampus by Bakker and colleagues (2008), who found pattern separation in the combined CA_3/DG region using high-resolution fMRI. These results and others were summarized in a landmark review paper by Yassa and Stark (2011), which noted the critical roles for CA_3 and DG in neural pattern separation.

One human fMRI study aimed to directly link the degree of neural pattern separation to the resolution of interference, demonstrating that learning increases neural pattern differentiation in the hippocampus, and that increased pattern differentiation leads to decreased interference (Favila et al., 2016). The same lab later used a spatial navigation task to demonstrate that highly similar events actually trigger a repulsion of hippocampal patterns, such that overlapping events invoke hippocampal patterns that are more distinct than those of non-overlapping events (Chanales et al., 2017). Thus, there is much evidence that neural pattern separation in hippocampal subfields CA_3 and DG leads to resolution of memory interference.

Interim Summary

To summarize our review of the rich history of interference literature: 1) proactive interference occurs when prior knowledge hinders learning of new information; 2) greater similarity of stimuli and/or context leads to greater interference; 3) proactive interference affects associative memory; and 4) the brain resolves interference via pattern separation in hippocampal subfields CA_3 and DG. There is overwhelming behavioral evidence for proactive interference's detrimental effect on learning. The advent of neuroimaging sparked inquiry into the brain's mechanisms for mitigating interference, and our understanding of these mechanisms has increased greatly in the past two decades. However, just as facilitation didn't tell the whole story, neither does interference. To fully understand how overlapping experiences affect learning and memory, facilitation and interference must be studied together. Despite this obvious need, there is limited research exploring these phenomena simultaneously.

Unified Investigations of Facilitation and Interference

Both facilitation and interference are well-established phenomena, yet they present seemingly contradictory ideas. How do overlapping experiences cause facilitation in some scenarios and interference in others? While research on both memory facilitation and interference have lengthy histories, only recently have researchers begun investigating them together. In one creative design, participants viewed 20 videos depicting navigation through one of two houses in which they came across 10 objects. Using pattern similarity analysis of hippocampal subfield activity recorded with fMRI, they found that neural patterns in left CA_1 were more similar for objects encountered in the same video, while patterns in left $CA_{2/3}$/DG were less similar for objects from the same video (Dimsdale-Zucker et al., 2018). While this demonstrates the co-occurrence of neural pattern integration and pattern separation, they did not

link the extent of pattern similarity in either region to behavioral performance, likely due to an insufficient sample size. Similarly, another study used an associative inference task to examine pattern similarity in hippocampal subfields, and found that memory reactivation led to pattern integration in CA_1 and pattern separation in $CA_{2/3}$/DG and subiculum (Molitor et al., 2021). Interestingly, they found that increased pattern similarity in subiculum improved task performance. Given that they found evidence for pattern separation in subiculum, this link to behavior raises more questions than it answers.

In another study, overlapping items in a paired-associates task caused facilitation in some participants and interference in others (Schlichting & Preston, 2014). After learning AB pairs, participants learned both overlapping BC pairs and non-overlapping XY pairs. Some participants performed better during a cued recall test for BC pairs, showing facilitation, while others performed better for XY pairs, showing interference. However, the distribution of the difference scores was roughly normally distributed around 0, indicating that most participants performed about equally well on overlapping BC pairs and non-overlapping XY pairs. While this study provides an interesting instance of facilitation and interference observed in the same task, this duality stemmed from individual differences as each participant experienced only one effect or the other, if either at all. Thus, the same participant did not experience both facilitation and interference within the same task.

In an attempt to observe both facilitation and interference behaviorally, one study used an associative inference task with different contexts, operationalized as background images during the task (Cox et al., 2021). They found evidence for memory integration when the context remained the same, while changing context led to interference relative to a control. While this study provides an interesting look into disparate effects on memory, it presents the contrast such

that overlap causes facilitation and no overlap causes interference, rather than both effects being caused by overlap. These studies have provided the foundation for a unified investigation of facilitation and interference. The next step needed to progress our understanding of these interrelated phenomena is to tease apart how overlapping experiences can cause both facilitation and interference.

Goal of Dissertation

The goal of this dissertation is to reconcile the well-established yet seemingly contradictory finding that overlapping experiences can both facilitate and hinder new learning. This chapter has reviewed existing literature on facilitation and interference. Chapter 2 details two empirical studies that introduce a novel behavioral task that elicits both interference and facilitation through two distinct types of overlap. This chapter is a published journal article, co-authored by Dr. Dasa Zeithamova. Chapter 3 provides a series of studies that replicate the findings from Chapter 2 while utilizing alternate response procedures. Chapter 4 explores the neural mechanisms underlying both facilitation and interference. Chapter 5 provides an integrated discussion, summarizing the findings of this dissertation and exploring future directions.

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CHAPTER II

DIFFERENTIAL EFFECTS OF LOCATION AND OBJECT OVERLAP ON NEW LEARNING

From Chaloupka, B. & Zeithamova, D. (2024). Differential effects of location and object overlap on new learning. *Frontiers in Cognition, 2*. https://doi.org/10.3389/fcogn.2023.1325246

Overlap of experiences can facilitate new learning by allowing us to integrate new experiences within an established framework. For example, imagine that you are visiting a friend's house for the first time. You are quickly able to orient yourself to the rooms in the house because you already have a framework, or schema, of how a house is laid out. You know that the kitchen and living room are likely on the ground level, the bedrooms are upstairs, and so on. In this case, your prior knowledge of houses facilitates your learning of the layout of your friend's house. However, overlap of experiences can also hinder new learning via proactive interference. Imagine that you head into your friend's kitchen to grab a spoon for a snack. You keep your utensils in the drawer next to the stove, but your friend keeps theirs in the drawer next to the dishwasher. Even after you find the utensils the first time, you keep going to the wrong drawer every time you come back to your friend's house. In this case, your prior knowledge (where you keep your utensils) interferes with your learning of the new information (where your friend keeps their utensils). How can overlap of experience facilitate new learning in some cases while hindering it in others?

Facilitation has often been studied in the context of schemas. A schema is a structured mental representation of a concept or other complex stimuli that allows us to quickly integrate new information into memory. The term 'schema' was first applied to the field of cognitive psychology by Bartlett, defining it as the mechanism of learning by which new experiences are overlaid upon prior experiences (1932). Attneave demonstrated that participants with prior

knowledge of two kinds of schemas – letter patterns and polygons – performed better on a paired-associates task compared to participants without prior knowledge of the schemas (1957). Building on this work, Posner and colleagues showed that the degree of overlap among stimuli directly related to the rate of new learning, such that learning was faster when overlap was higher (1967). These effects have been replicated across a plethora of contexts (van Kesteren et al., 2014; for a review, see van Kesteren et al., 2012) and modalities (King et al., 2019). While it has been thought that schemas take a long time to develop (Sommer, 2016), more recent research suggests that schemas may develop quickly, even when not called upon until the episodic memory for a specific event begins to fade (Tompary et al., 2020).

In a seminal study that brought schema research back into the spotlight, Tse and colleagues found that spatial schemas provide a framework that facilitates new learning in rats (2007). In this study, rats were trained over several months to learn six flavor-location associations in an arena, until they learned the associations well and presumably developed a spatial schema of the arena and all the relevant locations in it. Once a spatial schema was formed, two of the flavor targets were replaced by new flavors and moved to neighboring locations. The rats were given a single training trial in which the new flavor-location pairs were rewarded. Despite receiving only one trial to learn the new associations, the rats successfully learned and retained the new pairs. This indicates the facilitatory effect of a spatial schema on new learning. This pattern has been replicated in humans, demonstrating that an experimentally-learned spatial schema effectively facilitates new learning (van Buuren et al., 2014). Collectively, this research demonstrates that overlap with prior memories, particularly spatial schemas, can facilitate new learning.

An equally established consequence of an overlap with prior memories is interference. Specifically, proactive interference – the memory of old information hindering the learning of new information – was first described by Maslow nearly a century ago (1934). Later, Melton and von Lackum found that learning of consonant strings was slower when they overlapped highly with previously learned consonant strings (1941). This was one of the first studies that demonstrated that greater stimulus overlap leads to greater interference. Wickens and colleagues confirmed this effect by showing that proactive interference only persists so long as the stimuli are of a similar kind; switching stimuli types (consonant strings to number strings, or vice versa) did not lead to interference (1963). The finding that overlap with prior memories can hinder new learning has been extended to semantic categories (Wixted & Rohrer, 1993) and languages (Goggin & Wickens, 1971) and has been confirmed using a variety of tasks (Bunting, 2006; for a review, see Kliegl & Bäuml, 2021). Additionally, overlap can be detrimental to associative memory, as demonstrated in a classic AB/AC paradigm: after learning one set of paired-associates (AB), participants have greater difficulty learning a new set overlapping (AC) associations than non-overlapping (DE) associations (Caplan et al., 2022; Postman et al., 1974; Tulving & Watkins, 1974; Wahlheim & Jacoby, 2013). Taken together, these findings indicate that overlap with an existing memory makes it more difficult to encode a new one, and competition between two overlapping memories makes the retrieval of a target memory more difficult (Kuhl et al., 2007, 2011). Thus, a large body of work has demonstrated that overlap with prior memories can hinder learning.

As both the beneficial and detrimental effects of information overlap on new learning have been well documented, how can we reconcile these findings? As the schema research and interference research have proceeded largely in parallel, using distinct task paradigms, stimuli,

timing, length of training, etc., it is challenging to discern which differences are critical for the distinct behavioral outcomes—facilitation vs. interference—across studies. In the present study, we ask if it is possible to observe both facilitation and interference *within a single task* by manipulating *what* overlaps across experiences. Notably, many previous studies showing the facilitatory effect of overlap did so using overlap with spatial, conceptual, and relational schemas (Tse et al., 2007; van Buuren et al., 2014). In contrast, many previous studies showing the interference effect of overlap utilized list learning or associative memory paradigms (Bunting, 2006; Goggin & Wickens, 1971; Postman et al., 1974; Wickens et al., 1963; Wixted & Rohrer, 1993). We thus developed a novel object-location association task that allowed us to test the effect of two types of overlap, spatial locations and object set, within a single task. Participants learned one grid of object-location associations and then learned a second grid of object-location associations that overlapped with the first in objects and/or locations. Given prior work showing facilitatory effects of overlap with existing spatial schemas, we hypothesized that location overlap will facilitate new learning. In contrast, given prior work showing detrimental effect of overlap for word lists and object pairs, we hypothesized that object overlap will interfere with new learning. By manipulating these two factors together, we aim to bridge the gap between schema and interference research and reconcile the conflicting findings regarding the effect of overlap on memory. In a second experiment, we aim to replicate the findings from Experiment 1 and extend our findings by manipulating a third variable.

Experiment 1

Materials and Methods

Participants

Participants were recruited from the University of Oregon human subjects pool and received course credit for their participation. Informed consent was obtained from all participants, and experimental procedures were approved by Research Compliance Services at the University of Oregon. We recruited 102 in-person participants (79 female, 22 male, 1 other), age 18-25 years (M = 19.33, SD = 1.52). Four participants were excluded for failing to complete the task, and 13 were excluded for failing to learn at least one of the grids within the allotted number of trials. The target sample size was determined to be 160 based on a power analysis (α = .05, power = .80, partial η^2 = .05 estimated for each main effect). However, the COVID-19 pandemic halted in-person data collection before a full sample could be collected. Thus, we recruited an additional 273 online participants. Due to experimenter error in pivoting to online data collection amidst the pandemic, demographic information was not collected for the online participants. Since both in-person and online participants were recruited through introductory psychology courses at the University of Oregon, we are confident that the in-person demographic information collected is representative of the overall sample. Of the online sample, 50 were excluded from analyses for failing to complete the task or failure to follow instructions, 13 were excluded for failing to learn one or both grids, and 6 were excluded for failing to pass the attention check. After exclusions, 85 in-person participants and 204 online participants were included in all analyses, for a total of 289 participants. For brevity and clarity, we report analyses from the full sample, including both in-person and online participants. However, we also

analyzed the data with setting as an additional factor to verify that the pattern of results was the same for both the in-person sample and the online sample.

Procedure

Overview. Participants completed a novel grid learning task in which they learned grids of object-location associations. Each 8x8 grid contained eight objects in various locations throughout the grid (see Figure 2.1). Each participant sequentially learned two object-location grids, where the second grid would overlap with the first in the objects, locations, both, or neither. By measuring how long it took participants to learn each grid, we could evaluate if overlap in each of these factors was facilitatory or detrimental to new learning. The grid task was administered using PsychoPy (RRID:SCR_006571) for in-person participants and Pavlovia (RRID:SCR_023320) for online participants.

Stimuli. We combined two sets of objects and two sets of locations to create eight distinct grids to be used in the study. To create each location set, we pseudo-randomly selected locations from the grid, with the constraint that no location was selected at the border (edge of the grid) and no two locations were immediate neighbors vertically or horizontally (diagonal contact ok). Each object set was then randomly placed within each location set, for a total of four object-location grids. The objects in each of these grids were then randomly shuffled (with no object in the same location across the two grids) to create a second version of each object-location grid, for a total of eight possible grids used in the study across participants. All grids were constructed in Microsoft Excel (RRID:SCR_016137).

Participants were randomly assigned one of these grids to be their starting grid, and the starting grid was roughly counterbalanced across participants and conditions. Their second grid was chosen from the remaining grids based on the condition that the participant was randomly

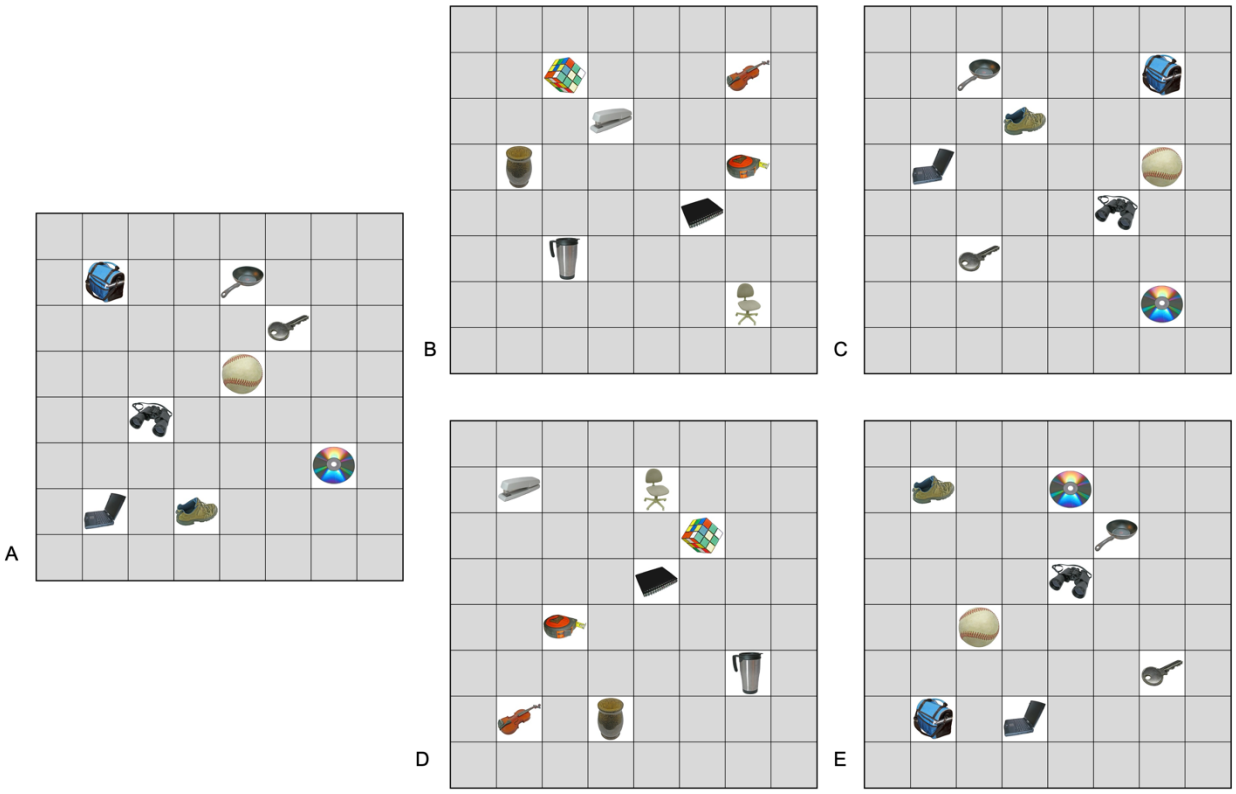

Figure 2.1. The grids of object-location associations used in Experiment 1. (A) Example starting grid. (B) No overlap condition; different stimulus set and locations. (C) Object overlap condition; same stimulus set in different locations. (D) Location overlap condition; different stimulus set but same locations. (E) Full overlap condition; same stimulus set and locations. Images used in this figure are unaltered images from the BOSS stimulus sets (Brodeur et al., 2010; Brodeur et al., 2014) used under the Creative Commons Attribution License (https://creativecommons.org/licenses/by-sa/3.0/).

assigned to (see Figure 2.1). In the no overlap control group, the second grid used a new set of objects and a new set of locations (Fig. 2.1B). In the object overlap group, the second grid contained the same set of objects, but placed in a new set of locations (Fig. 2.1C). In the location overlap group, the second grid contained a new set of objects, but in the same locations as the first grid (Fig. 2.1D). In the full overlap group, the second grid used the same set of objects and the same set of locations, but the objects were shuffled so that the grids were not identical (Fig. 2.1E).

Grid Learning. First, participants learned their starting grid. The grid learning procedure is depicted in Figure 2.2A and was the same for Grid 1 and Grid 2 (Figure 2.2B). The grid was displayed on screen for 8 s followed by 4 s of a fixation cross. Then, a blank grid appeared with the eight objects displayed beneath the grid. Participants attempted to recreate the grid by dragging and dropping the objects to their correct locations within the blank grid. The test was self-paced. Participants submitted each attempt by pressing the spacebar. Following each attempt, participants received feedback in the form of the number of correctly placed objects (out of eight). If all eight objects were correctly placed, they moved on to the next phase of the task. Otherwise, they repeated this process until they correctly placed all eight objects with a maximum of eight attempts. We recorded the number of trials it took each participant to learn the

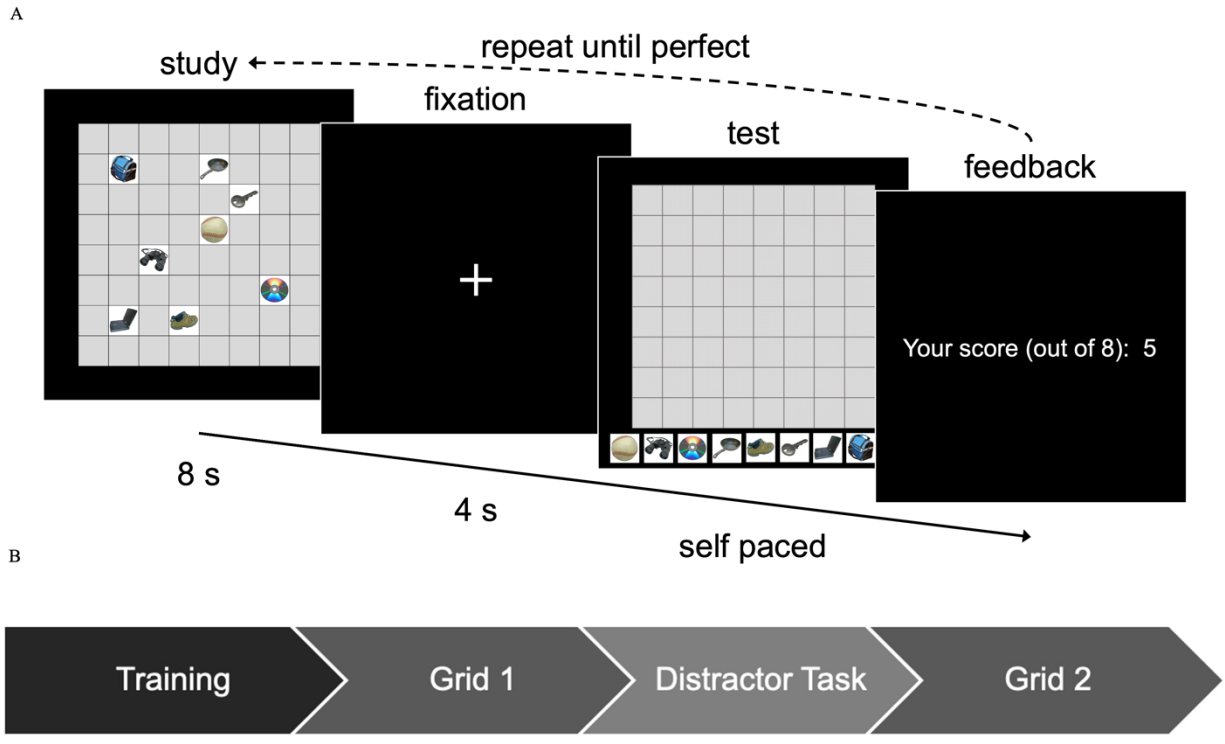

Figure 2.2. Grid learning task used in Experiment 1. (A) Participants learned each of the two grids using this process. (B) Overview of the timeline of the grid task. Images used in this figure are unaltered images from the BOSS stimulus sets (Brodeur et al., 2010; Brodeur et al., 2014) used under the Creative Commons Attribution License (https://creativecommons.org/licenses/by-sa/3.0/).

grid. The duration of each grid (8 s) and the maximum number of trials to learn the grid (8 attempts) was based on pilot data collection to ensure that the majority of participants need more than 1 attempt but fewer than 8 attempts to learn. Participants who failed to learn the grid after eight attempts were categorized as 'non-learners' and excluded from analysis. Prior to the actual task, participants received instructions and practiced the task using a simplified training grid with just two objects (not used in the main experiment).

Math Distractor Task. Next, participants completed a math distractor task. On each trial, participants were shown a simple arithmetic expression and asked to evaluate if the expression was true or false using the 'T' and 'F' keys, respectively. For example, "3 + 5 = 9" required a response of 'F'. Each arithmetic problem was displayed on screen for 4 s during which participants made their response. They then received feedback on screen for 2 s indicating if they were correct, incorrect, or too slow to respond. Participants completed 20 trials for a total of 2 min. This served as an attention check and working memory flush, preventing participants from actively rehearsing the previously learned grid. To ensure engagement, participants with less that 75% accuracy on this task were excluded from analyses.

Second Grid Learning. Following the math distractor task, participants learned their second grid using the same procedure as the first. Participants were randomly assigned to one of four groups, dictating whether Grid 2 overlaps with the previously learned Grid 1 in objects, locations, both objects and locations, or neither objects nor location (Figure 2.1). In addition to recording the number of trials it took for each participant to learn Grid 2, we also calculated the difference in the number of trials to learn the two grids by subtracting the number of trials to learn the second grid from the number of trials to learn the first grid (Grid 1 minus Grid 2). Thus, a difference score of 0 indicated that they took the same number of trials to learn both grids, a

positive score meant that they learned the second grid faster (in fewer trials) than the first, and a negative number indicated that they learned the second grid slower (needing more trials) than the first.

Additional Cognitive Measures. In addition to the grid task, only the in-person participants also completed a short battery of cognitive tasks (visual working memory capacity measure: Adam et al., 2015; reading span: first developed by Daneman & Carpenter, 1980, adapted from Unsworth et al., 2005; and Raven's advanced progressive matrices: Verguts & Boeck, 2002) for a pilot project not discussed in this paper. The reading span task was administered using PsychoPy, while the visual working memory task and Raven's advanced progressive matrices were administered using MATLAB. Given that less than a third of the final sample had these measures collected, they were not used in any subsequent analyses.

Results

First, we measured the number of trials to learn the first grid (M = 4.23, SD = 1.68). Since this grid was learned prior to experimental manipulation, we predicted no significant differences between groups. To test this, we ran a 2x2 (object overlap x location overlap) factorial ANOVA with the number of trials to learn the first grid as the dependent variable (Figure 2.3A). As expected, we found no main effect of object overlap, $F(1, 285) = 0.02$, $p = .882$, $\eta_p^2 = .00$, no main effect of location overlap, $F(1, 285) = 2.13$, $p = .146$, $\eta_p^2 = .01$, and no interaction, $F(1, 285) = 0.62$, $p = .431$, $\eta_p^2 = .00$, confirming that there were no between-group differences prior to experimental manipulation.

Of main interest, we measured the number of trials to learn the second grid (M = 3.15, SD = 1.58) as well as the within-subject difference in the number of trials to learn the second grid in comparison to the first grid. We hypothesized that object overlap would cause interference,

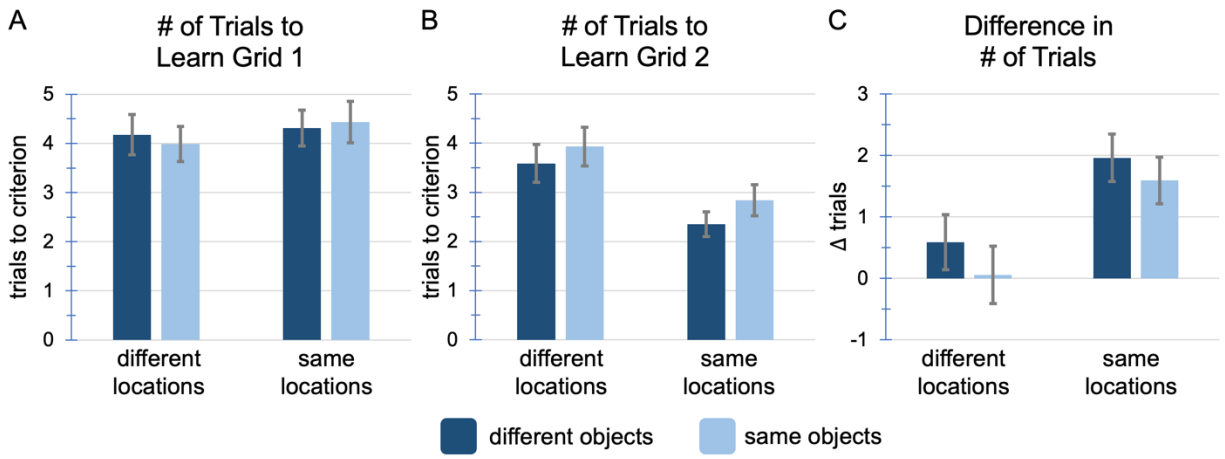

Figure 2.3. Results of Experiment 1. (A) The number of trials to learn the first grid by condition, prior to any manipulation. There was no main effect of object overlap (p = .882), no main effect of location overlap (p = .146), and no interaction (p = .431). (B) The number of trials to learn the second grid by condition, after manipulation. There was a main effect of object overlap (p = .016), a main effect of location overlap (p < .001), and no interaction (p = .667). (C) The difference between the number of trials to learn the two grids (grid 1 – grid 2). A positive number indicates faster learning of grid 2. There was a main effect of object overlap (p = .038), a main effect of location overlap (p < .001), and no interaction (p = .703). Error bars represent 95% confidence intervals for all plots.

resulting in a greater number of trials to learn the second grid, while location overlap would cause facilitation, resulting in fewer trials to learn the second grid. To test this hypothesis, we ran a 2x2 (object overlap x location overlap) factorial ANOVA with the number of trials to learn the second grid as the dependent variable (Figure 2.3B). Consistent with our hypothesis, we found a main effect of object overlap, $F(1, 285) = 5.91$, $p = .016$, $\eta_p^2 = .02$, driven by fewer trials required to learn the second grid when *objects did not overlap* ($M = 2.92$, $SD = 1.51$) compared to when *objects did overlap* ($M = 3.40$, $SD = 1.63$). We also found a main effect of location overlap, $F(1, 285) = 45.81$, $p < .001$, $\eta_p^2 = .14$, driven by fewer trials required to learn the second grid when *locations did overlap* ($M = 2.58$, $SD = 1.25$) compared to when *locations did not overlap* ($M = 3.76$, $SD = 1.67$). These results indicate that overlap with prior experience can have

dissociable effects, depending on the type of overlap. There was no interaction, $F(1, 285) = 0.19$, $p = .667$, $\eta_p^2 = .00$, indicating that the main effects were independent and additive.

To ensure that these effects were not driven by individual differences in grid learning ability, we calculated the difference in the number of trials to learn the two grids by subtracting the number of trials to learn the second grid from the number of trials to learn the first grid (Figure 2.3C). A score of 0 would indicate that a participant took the same number of trials to learn both grids, a positive score that they learned the second grid faster than the first, and a negative score would indicate that they learned the second grid slower than the first. Averaged across conditions, participants showed practice effects, learning the second grid about one trial faster than the first ($M = 1.08$, $SD = 1.98$), with overall 63% of participants improving from the first to the second grid. However, the magnitude of the practice effect varied across conditions. A 2x2 factorial ANOVA with the difference score as the dependent variable replicated a main effect of object overlap, $F(1, 285) = 4.33$, $p = .038$, $\eta_p^2 = .015$, driven by greater improvement across grids when *objects did not overlap* ($M = 1.33$, $SD = 1.94$) compared to when *objects did overlap* ($M = 0.81$, $SD = 1.99$). When *objects did not overlap*, 68% of participants improved, learning the second grid in fewer trials than the first, while only 57% of participants improved when *objects did overlap*, $\chi^2(1, N = 289) = 3.61$, $p = .057$. We also found a main effect of location overlap, $F(1, 285) = 45.62$, $p < .001$, $\eta_p^2 = .14$, driven by greater improvement across grids when *locations did overlap* ($M = 1.79$, $SD = 1.70$) compared to when *locations did not overlap* ($M = 0.31$, $SD = 1.97$). When *locations did overlap*, 77% of participants improved, learning the second grid in fewer trials, while only 48% of the participants improved when *locations did not overlap*, $\chi^2(1, N = 289) = 26.62$, $p < .001$. There was no interaction, $F(1, 285) = 0.15$, $p = .703$, $\eta_p^2 = .00$, confirming that the main effects were independent and additive.

To verify that these results were not affected by setting, we also conducted all the analyses with setting (in-person, online) as an additional between-subjects factor. In all analyses, we found a main effect of setting (all p's < .04). Online participants learned the first grid about 1 trial faster and second grid about 0.5 trials faster. Importantly, setting did not interact with any other factor and the main effects of location and object overlap remained the same.

Discussion

In Experiment 1, we wanted to know if location overlap and object overlap would have opposing effects, and if we could observe both effects within a single task. In line with our hypotheses, we found in an object-location associative learning task that location overlap facilitates new learning while object overlap hinders new learning. Additionally, our results indicate that these effects are independent and additive. While we found significant main effects of both facilitation and interference, the magnitude of the interference effect was rather small, with η_p^2 at 0.01-0.02. Thus, we conducted a second experiment to replicate these findings. Given that observing changes in the number of trials to criterion, each constrained between 1 and 8, provides a relatively coarse measure of learning, we reduced the exposure time and increased the maximum number of attempts to ten in the second experiment. If we again observe both facilitation and interference effects in a separate sample, we can conclude that they are robust, even if the effect size of the interference effect is small.

Additionally, our findings led us to inquire as to how these effects would hold up to context shifts, operationalized as a change of the shape of the grid. On one hand, when the context, or the shape of one's environment changes, hippocampal place cell representations undergo remapping, as observed in both rodents (Lever et al., 2002; Wills et al., 2005) and more recently humans (Wanjia et al., 2021). Across two different contexts, the same relative locations

are represented by a different set of hippocampal neurons. However, it is possible that the learned spatial pattern may itself become the context, or schema. For example, people may remember the configuration of locations from the first grid, utilizing that information when it overlaps in the second grid. In this case, overlap of the spatial pattern may supersede a shift in grid shape and the facilitatory effect of location overlap would generalize.

Interference effects are also modulated by shifts in context. Specifically, interference effects caused by stimulus overlap can be eliminated by shifting contexts or stimulus types (Bunting, 2006; Goggin & Wickens, 1971; Unsworth et al., 2013; Wixted & Rohrer, 1993). Stimulus overlap may no longer be detrimental to new learning when the context changes. To explore these questions in Experiment 2, we created two distinct grid shapes to operationalize a change in the environment. We then explicitly tested whether changing the grid shape eliminates the facilitatory effect of location overlap and/or the interference effect of object overlap, or if these effects are preserved.

Experiment 2

Materials and Methods

Participants

Participants were recruited from the University of Oregon human subjects pool and received course credit for their participation. Informed consent was obtained from all participants and experimental procedures were approved by Research Compliance Services at the University of Oregon. All participants completed the task online. We recruited 534 participants; 102 participants were excluded for failing to complete the task, 4 were excluded for failing to learn at least one of the grids within the allotted number of trials, 21 were excluded for failing to pass the attention check, and 17 were excluded for learning the first grid on the first trial (see below). The

remaining 390 participants were used in the following analyses. In Experiment 1, we conducted a power estimate using a medium effect size since there was no directly related prior research from which to base the estimate on. However, the actual effect size for object overlap was smaller. In Experiment 2, we used the effect size from Experiment 1 to motivate our power analysis. The target sample size was determined to be 387 based on a power analysis (α = .05, power = .80, partial η^2 = .02 estimated for each main effect, based on the results from Experiment 1). Due to experimenter error in pivoting to online data collection amidst the pandemic, demographic information was not collected for these participants. Since all participants were recruited through introductory psychology courses at the University of Oregon, we are confident that the demographic information reported in Experiment 1 is representative of the overall sample.

Procedure

Overview. The task procedure was largely the same as in Experiment 1. The grid task was administered online using Pavlovia (RRID:SCR_023320).

Stimuli. Here, we manipulated a third factor: grid shape. We used two distinct grid shapes. To construct the shapes, we started with an 8x8 grid and then eliminated two squares on each side. For the first shape, we removed the two center squares on each edge, creating an 'x'-like shape. For the second shape, we removed each corner square as well as one adjacent square immediately counterclockwise to each corner, creating a 't'-like shape (see Figure 2.4). As in Experiment 1, we constructed two unique grids for each grid shape, object set, and location set to allow for the full overlap condition, resulting in 16 total grids. As in Experiment 1, all grids were constructed in Microsoft Excel (RRID:SCR_016137). Participants were randomly assigned one of these grids to be their starting grid, and the starting grid was roughly counterbalanced across

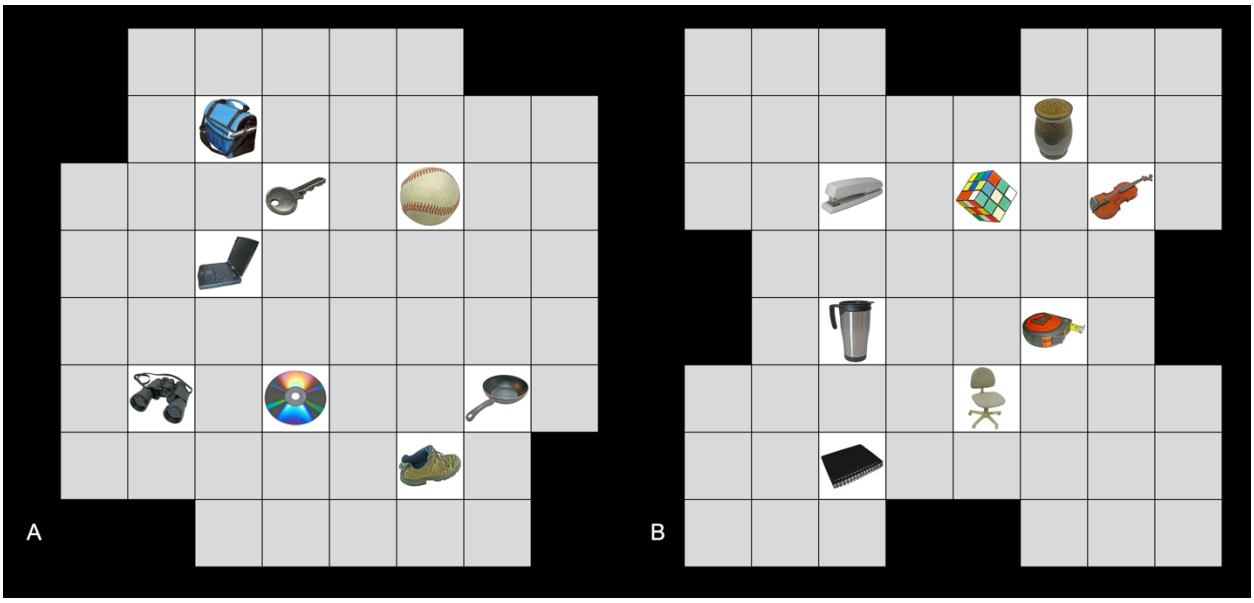

Figure 2.4. Example grids from Experiment 2. (A) An example grid with one set of objects, one set of locations, and the 't' grid shape. (B) An example grid with the other set of objects, the other set of locations, and the 'x' grid shape. Images used in this figure are unaltered images from the BOSS stimulus sets (Brodeur et al., 2010; Brodeur et al., 2014) used under the Creative Commons Attribution License (https://creativecommons.org/licenses/by-sa/3.0/).

participants and conditions. Their second grid was chosen from the remaining grids based on the condition that the participant was randomly assigned to.

Grid Learning. The learning procedure was similar but not identical to Experiment 1. The grids were displayed on screen for 6 s instead of 8 s, and the maximum number of attempts to learn each grid was increased from 8 to 10. We also included an additional exclusion criterion based on the data from the online sample from Experiment 1. We noticed that several participants learned the first grid in a single trial. While it is possible for participants with exceptional memory abilities to achieve such a feat, it is unlikely and had not occurred in the in-person sample. We suspected that participants may be taking a picture of the grid and using that to reconstruct the grid. Thus, we excluded from analyses any participants who learned the first grid in a single trial but verified that the pattern of the results would be the same regardless. Besides these changes, the rest of the task remained the same as in Experiment 1.

Results

First, we measured the number of trials to learn the first grid (M = 3.85, SD = 1.57). Since this grid was learned prior to experimental manipulation, we predicted no significant differences between groups. To test this, we ran a 2x2x2 (object overlap x location overlap x grid shape) factorial ANOVA with the number of trials to learn the first grid as the dependent variable (Figure 2.5A; Table 2.1). As expected, we found no significant main effects or interactions, confirming that there were no between-group differences prior to experimental manipulation.

Next, we measured the number of trials to learn the second grid (M = 3.07, SD = 1.58). We hypothesized that object overlap would cause interference, resulting in a greater number of trials to learn the second grid, while location overlap would cause facilitation, resulting in fewer trials to learn the second grid. We did not have a strong prediction regarding the effect of grid shape. However, we were interested in the interaction between object overlap and grid shape. If a change in grid shape resulted in a release from proactive interference, we would expect to see an interaction between object overlap and grid shape. However, if proactive interference persists across grid shapes, then we would not expect to find an interaction. We were also interested in the interaction between location overlap and grid shape. If a change in grid shape causes spatial

Table 2.1

Experiment 2 ANOVA Table with the Number of Trials to Learn Grid 1 as the Dependent Variable and Location Overlap, Object Overlap, and Grid Shape Overlap as Independent Variables

Predictor	SS	*df*	MS	*F*	*p*	η_p^2
location overlap	0.04	1	0.04	0.02	.900	0.00
object overlap	0.29	1	0.29	0.11	.736	0.00
grid shape	0.77	1	0.77	0.31	.579	0.00
location overlap * object overlap	0.03	1	0.03	0.01	.920	0.00
location overlap * grid shape	0.74	1	0.74	0.30	.586	0.00
object overlap * grid shape	0.82	1	0.82	0.33	.567	0.00
location overlap * object overlap * grid shape	0.01	1	0.01	0.01	.941	0.00
Residuals	953.89	382	2.50			

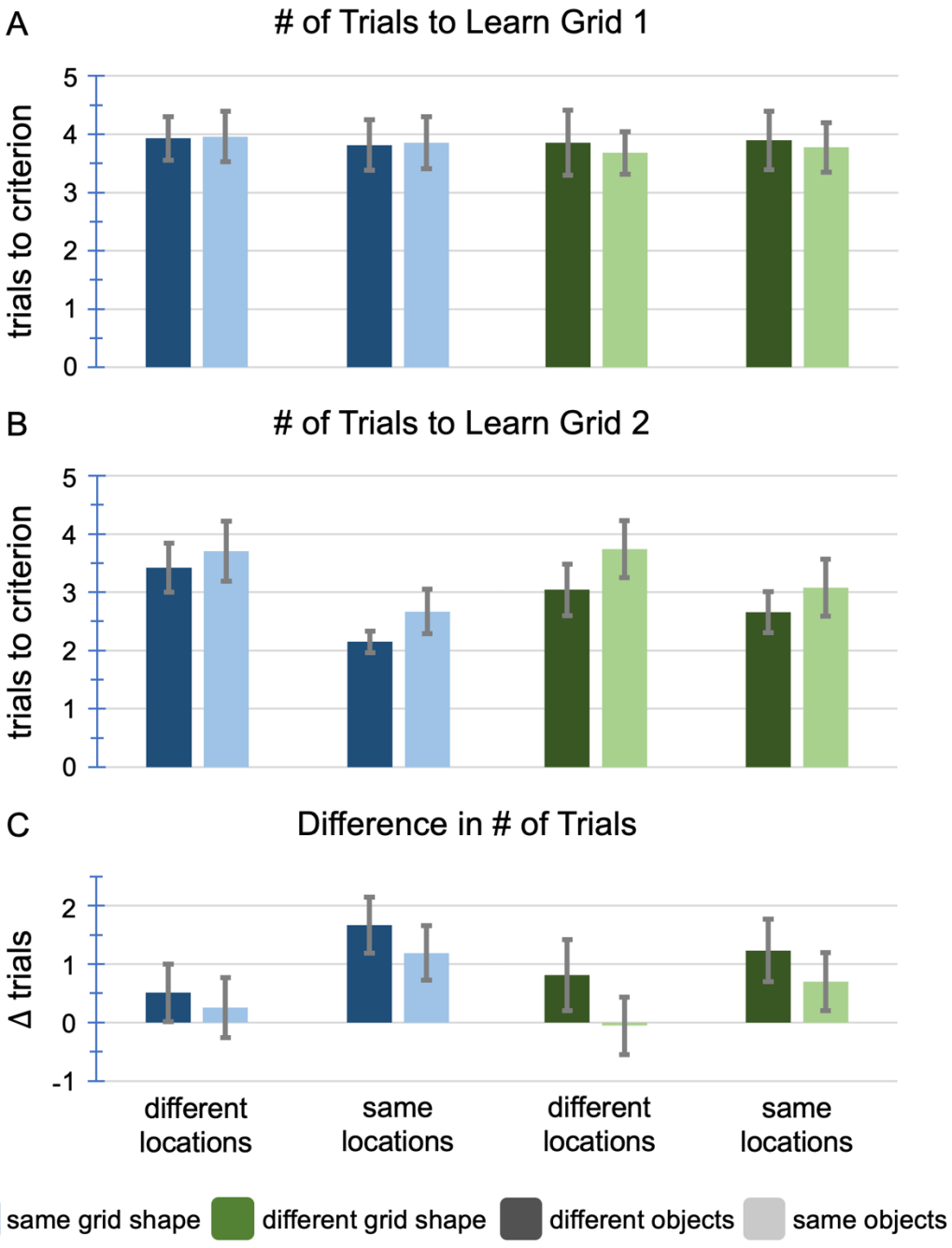

Figure 2.5. Results of Experiment 2. (A) The number of trials to learn the first grid by condition, prior to any manipulation. There were no significant differences. (B) The number of trials to learn the second grid by condition, after manipulation. There was a main effect of object overlap ($p = .002$), a main effect of location overlap ($p < .001$), and an interaction between location overlap and grid shape ($p = .039$). (C) The difference between the number of trials to learn the two grids (grid 1 – grid 2), accounting for individual differences. There was a main effect of object overlap ($p = .005$), and a main effect of location overlap ($p < .001$). Error bars represent 95% confidence intervals for all plots.

remapping, we would expect to see an interaction between location overlap and grid shape. However, if the facilitatory effect of location overlap persists across grid shapes, then it suggests that participants remember the overall configuration of locations rather than the locations with respect to the grid edges. To test these hypotheses, we ran a 2x2x2 (object overlap x location overlap x grid shape) factorial ANOVA with the number of trials to learn the second grid as the dependent variable (Figure 2.5B, Table 2.2). Consistent with Experiment 1, we found a main effect of object overlap, driven by fewer trials required to learn the second grid when *objects did not overlap* ($M = 2.82$, $SD = 1.39$) compared to when *objects did overlap* ($M = 3.34$, $SD = 1.72$). We also found a main effect of location overlap, driven by fewer trials required to learn the second grid when *locations did overlap* ($M = 2.60$, $SD = 1.24$) compared to when *locations did not overlap* ($M = 3.48$, $SD = 1.73$). We found no main effect of grid shape. However, we found a significant interaction between location overlap and grid shape, such that the magnitude of the facilitatory effect of location overlap was larger when the grid shape remained the same, but smaller when the grid shape changed.

To ensure that these effects were not driven by individual differences in grid learning ability, we calculated the difference in the number of trials to learn the two grids by subtracting

Table 2.2

Experiment 2 ANOVA Table with the Number of Trials to Learn Grid 2 as the Dependent Variable and Location Overlap, Object Overlap, and Grid Shape Overlap as Independent Variables

Predictor	SS	*df*	MS	*F*	*p*	η_p^2
location overlap	67.65	1	67.65	30.20***	< .001	0.07
object overlap	22.10	1	22.10	9.87**	.002	0.03
grid shape	1.98	1	1.98	0.88	.348	0.00
location overlap * object overlap	0.01	1	0.01	0.01	.937	0.00
location overlap * grid shape	9.65	1	9.65	4.31*	.039	0.01
object overlap * grid shape	0.55	1	0.55	0.25	.619	0.00
location overlap * object overlap * grid shape	1.56	1	1.56	0.70	.404	0.00
Residuals	855.66	382	2.24			

*$p < .05$. **$p < .01$. ***$p < .001$.

the number of trials to learn the second grid from the number of trials to learn the first grid, as in Experiment 1. Averaged across conditions, participants showed practice effects, learning the second grid nearly one trial faster than the first (M = 0.78, SD = 1.90). Overall, 56% of participants improved from the first grid to the second grid. However, the magnitude of the practice effect varied across conditions. We ran a 2x2x2 (object overlap x location overlap x grid shape) factorial ANOVA with the difference score as the dependent variable (Figure 2.5C; Table 2.3). We replicated the main effect of object overlap, driven by greater improvement across grids when *objects did not overlap* (M = 1.05, SD = 1.96) compared to when *objects did overlap* (M = 0.47, SD = 1.78). When *objects did not overlap*, 61% of participants improved, learning the second grid in fewer trials than the first, while only 50% of participants improved when *objects did overlap*, $\chi^2(1, N = 390) = 4.58$, $p = .032$. We also replicated the main effect of location overlap, driven by greater improvement across grids when *locations did overlap* (M = 1.23, SD = 1.75) compared to when *locations did not overlap* (M = 0.37, SD = 1.94). When *locations did overlap*, 66% of participants improved, learning the second grid in fewer trials, while only 46% of the participants improved when *locations did not overlap*, $\chi^2(1, N = 390) = 15.34$, $p < .001$. Controlling for individual differences, we no longer found a significant interaction between

Table 2.3

Experiment 2 ANOVA Table with the Difference in the Number of Trials to Learn the Two Grids as the Dependent Variable and Location Overlap, Object Overlap, and Grid Shape Overlap as Independent Variables

Predictor	SS	*df*	MS	*F*	*p*	η_p^2
location overlap	64.43	1	64.43	19.16***	< .001	0.05
object overlap	27.41	1	27.41	8.15**	.005	0.02
grid shape	5.22	1	5.22	1.55	.214	0.00
location overlap * object overlap	0.08	1	0.08	0.02	.880	0.00
location overlap * grid shape	5.04	1	5.04	1.50	.222	0.00
object overlap * grid shape	2.73	1	2.73	0.81	.369	0.00
location overlap * object overlap * grid shape	1.87	1	1.87	0.56	.457	0.00
Residuals	1284.88	382	3.36			

*$p < .05$. **$p < .01$. ***$p < .001$.

location overlap and grid shape, suggesting that the facilitatory effect of location overlap persisted across grid shapes. The magnitude of the effect was still numerically larger when the grid shape remained the same (d = 0.57) compared to when the grid shape changed (d = 0.32; Figure 2.5C), but post-hoc comparisons between location overlap and no location overlap for both the same grid shape and different grid shapes reached significance. We again found no main effect of grid shape and no other interactions. These comparisons replicated findings from Experiment 1 that location overlap leads to facilitation of learning the second grid while object overlap hinders learning of the second grid. In addition, they demonstrate that these effects remain largely stable across grid shapes.

Discussion

In Experiment 2, we aimed to replicate the results of Experiment 1 and test the degree to which the effect of location and content overlap are modulated when the overall shape of the grid is altered. First, the results largely replicated Experiment 1. Location overlap provided clear facilitation of learning the second grid. The interference effect driven by object overlap remained relatively small with η_p^2 at 0.02-0.03, but its replication across two studies indicates it is statistically reliable. Furthermore, in both Experiment 1 and Experiment 2, about 10% fewer participants improved across grids when objects overlapped. Thus, the interference effects can be seen in both quantitative (mean number of trials) and qualitative (improvement or not) measures of learning.

Experiment 2 also explored to what degree these effects are modulated by or robust to a change of the overall grid shape. We found that the shift in grid shape did not eliminate the proactive interference observed due to object overlap. This indicates that changing the grid shape was not comparable to shifts in context used in prior studies. When controlling for individual

variability, we also found that the shift in grid shape did not eliminate the facilitatory effect of location overlap. This suggests that the change in grid shape did not induce remapping in our participants, since the spatial pattern was similarly beneficial even in a new grid shape. Thus, we replicated our findings from Experiment 1 while also demonstrating that these effects generalize across grid shapes.

General Discussion

Prior work has shown both beneficial and detrimental effects of information overlap on new learning. Here, we tested whether both consequences of overlap can be observed in a single task by manipulating two types of overlap: spatial (locations) and content (objects) in an object-location associative learning task. Across two experiments, we demonstrated that location overlap facilitates new learning while object overlap hinders new learning. When controlling for individual variability by focusing on the change in the number of trials one needs to learn two grids, we found in Experiment 2 that these effects were largely preserved even when the grid shape changed. Taken together, our findings identify a key factor that determines the behavioral consequences of overlap and indicate a differential role of *what information* and *where information* in memory organization. Associating a second object with one location was easy for participants; associating a second location with one object presented a challenge.

Critically, our study is one of the first to dissociate the effects of these two distinct types of information overlap on new learning within the same task. The AB/AC task consisting of overlapping word-word or image-image associations is a classic paradigm for demonstrating interference resulting from overlap (for a review, see Kliegl & Bäuml, 2021). Recently, this paradigm was used to examine both memory enhancement and impairment by manipulating context using a background scene (Cox et al., 2021). In the present study, we modified this

paradigm to use object-location associations and demonstrated that the detrimental effect of overlap is not universal. Consistent with prior work, when the overlapping (A) items were objects, new learning was hindered. This effect is consistent with interference theory: overlapping objects (*what information*) caused proactive interference. Here, we newly demonstrate that the detrimental effect of content overlap generalizes to a situation that requires associating content with their spatial locations. However, when the overlapping (A) information involved locations (*where information*), new learning was facilitated rather than impaired. Thus, it is possible to manipulate the direction of the effect of overlap (facilitation or interference) within a single task by varying the type of information – content or spatial context – that overlaps across experiences.

Inspired by research on spatial and conceptual schemas, we hypothesized that location overlap would facilitate new learning. We indeed found a strong facilitation of subsequent learning by location overlap, despite our task differing in several ways from traditional schema research. While further research is needed to determine the mechanisms underpinning our findings, here we speculate that given the fixed relationship of the locations to each other in space, participants may form a generalized representation, or schema, of the location information. The object information can then be mapped onto this representation. During learning of the second grid in the location overlap condition, participants benefit from being able to "slot" new objects into the same spatial schema, similarly to how method of loci benefits memory for new material by associating it with familiar spatial locations (Ross & Lawrence, 1968; Wang & Thomas, 2000). This interpretation aligns with other work showing that spatial schemas can facilitate rapid new learning, as demonstrated in rodents by Tse and colleagues (2007, 2011) and in humans by van Buuren and colleagues (2014). The present study expands on

this prior work by showing that memories of spatial configurations, which may be early formations of spatial schemas, also facilitate new learning even when all objects are swapped out. This argument is strengthened by the results of Experiment 2. The facilitatory effect of location overlap was preserved across two distinct grid shapes, suggesting that participants encoded the configural organization of the target locations rather than individual locations with respect to the grid border. Thus, the spatial pattern itself may serve as the context, or schema.

The work on spatial schemas served as a key motivation for our study and our predictions regarding facilitation driven by location overlap. However, one concern regarding interpretation of our data in the schema framework is the speed at which a spatial schema can be learned. In prior work (Tse et al., 2007; van Buuren et al., 2014), participants learned the spatial schemas over multiple sessions spanning days or weeks. In a more extreme case, Sommer utilized a 302-day study design in which participants learned a semantic schema (2016). Despite the long-term acquisition phases used in these studies, more recent work has suggested that schemas may actually be learned quite quickly (Tompary et al., 2020). However, we typically rely on episodic memories until those memories fade, at which time we begin to rely on schemas and generalized memories. This leads us to believe that in the present study, participants may be acquiring a spatial schema while learning the first grid, and this potential schema facilitates their learning of the second grid when the locations, and thus the spatial schema, overlap. Of course, one may also consider the benefits of remembering the spatial configuration of locations without considering such a configuration to be a spatial schema. Future research is needed to determine if the current findings are best understood in terms of spatial schema or rather reflect some other process. Nonetheless, these findings provide further evidence that spatial information holds a unique role in memory organization (Arnold et al., 2011; Robin et al., 2016; Sheldon & Chu, 2017).

One limitation of the current paradigm is the location-emphasizing test response modality, asking participants to drag and drop provided objects to their location. Although this does not explain the opposing effects of content and location overlap, it may have led to extra-large benefit of location overlap (greatly reducing the number of locations that need to be considered) that may become more modest with a different type of object-location association test. Thus, future research should replicate the current findings with a wider range of memory probes. Another finding that should be revisited in future studies is the preservation of the facilitation and interference effects across a change in the overall grid shape. Participants may have been less affected by the change in grid shape in the current study because no location adjacent to the border was used for object placement, making it more likely that participants encode the overall spatial configuration of locations with limited reference to the grid border. It is possible that a stronger interaction with grid shape would be observed if border locations were used, especially if a location were to touch the border in one grid but not the other.

The interference and facilitation effects of object and location overlap observed here may also inform conflicting theories regarding how overlapping events are represented in the hippocampus, a key memory structure, to support memory. Facilitatory effects of overlap are thought to stem from incorporating new memories into existing memory representations through memory integration (Zeithamova et al., 2012) and schema-related memory (Gilboa & Marlatte, 2017; Guo & Yang, 2020; Preston & Eichenbaum, 2013). As such, increased similarity of neural representations leads to better memory of overlapping events (Schlichting et al., 2014; Takeuchi et al., 2022; Tse et al., 2007). In contrast, interference research has proposed an opposite representational strategy—minimizing similarity of neural representations—leading to better memory of overlapping events. Specifically, hippocampal pattern separation (Lohnas et al.,

2018; for a review, see Yassa & Stark, 2011) or repulsion (Chanales et al., 2017, 2021; Favila et al., 2016) improves memory by representing similar events by distinct neural codes to minimize interference. The current findings suggests that both integration and separation may benefit memory depending on behavioral consequences of overlap, leading to intriguing questions for future research regarding how the hippocampus will respond when faced with both the positive and negative effects of overlap in the same task.

In summary, we developed a novel paradigm where both positive and negative effects of information overlap on new learning can be demonstrated within the same task. We demonstrated that a key factor determining the behavioral consequences of overlap is the nature of the overlap: location overlap led to facilitation, object overlap led to interference. Additionally, these effects persisted across two distinct grid shapes. These findings help reconcile prior conflicting research on how overlap affects memory and offer a new paradigm to study both facilitation and interference within the same task. More broadly, the opposing effects of object overlap and location overlap demonstrate qualitative differences in the processing of content and spatial information, informing theories on the distinct roles of *what* and *where* in the organization of memory.

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CHAPTER III

DISPARATE EFFECTS OF OVERLAP GENERALIZE ACROSS RESPONSE PROCEDURES

Until recently, research on facilitation and interference in learning and memory have been conducted separately, leading to disparate claims of the effect of overlapping experiences. On one hand, research suggests that overlap facilitates new learning, often via schemas (Attneave, 1957; Bartlett, 1932; King et al., 2019; Posner et al., 1967; Sommer, 2016; Tompary et al., 2020; van Kesteren et al., 2014). A schema can be defined as a structured mental representation of a concept or other complex stimuli that allows us to quickly integrate new information into memory. In the past two decades, a substantial body of work demonstrates that spatial schemas are particularly effective at facilitating learning (Guo & Yang, 2020; Kyle et al., 2015; Tse et al., 2007; van Buuren et al., 2014). Thus, the facilitatory effect of overlap on new learning is a well-established finding.

On the other hand, a separate line of research suggests that overlapping experiences hinder new learning via interference (Bunting, 2006; Dallet & Wilcox, 1968; Goggin & Wickens, 1971; Keppel & Underwood, 1962; Maslow, 1934; Melton & von Lackum, 1941; Underwood, 1957; Wickens et al., 1963; Wixted & Rohrer, 1993). Interference can be proactive – when memories of previously learned information hinder the learning of new information – or retroactive – when the learning of new information hinders the memory of previously learned information. Overlapping experiences can interfere with associative memory in addition to just individual items (Kliegl & Bäuml, 2021; Postman et al., 1974; Tulving & Watkins, 1974). Thus, the interference effect of overlap on learning is also a well-established finding.

Only recently have these two lines of research been merged together (Cox et al., 2021; Dimsdale-Zucker et al., 2018; Molitor et al., 2021), yet none of these studies examine both

facilitation and interference as an outcome of overlap. Using a novel object-location association grid task, we demonstrated that overlapping locations facilitated new learning while overlapping objects hindered new learning via interference (Chaloupka & Zeithamova, 2024). This task, detailed in Chapter 2, successfully elicited both facilitation and interference by manipulating the *type* of overlap. This study dissociates the effects of overlapping *where information* from *what information*, shedding some light on the nuances of how overlap affects new learning.

Despite the promise of this task, there are some concerns with the original task design. The findings in Chapter 2 suggest that memory generalization, possibly a spatial schema, is responsible for the facilitatory effect when locations overlapped. However, the drag-and-drop procedure may create an inherent advantage for spatial information, rendering the effect trivial. Additionally, the manipulated factors are not balanced during the response phase. Participants are given all eight of the objects at the bottom of the screen, while they have 64 possible location options (or 36 if they figure out that the outer edge is never used). Thus, this imbalance could influence the effects of location and object overlap on new learning.

The present chapter aims to address these concerns by implementing a modified version of the grid task. In this version, we manipulated a third factor: test type. In place of the drag-and-drop procedure, we implemented a memory probe with two types to balance the response options. The new design alleviates the aforementioned concerns in two ways. First, participants are no longer using a drag-and-drop response. The new task uses a simple four-alternative forced-choice (4-AFC) procedure that draws no special attention to the spatial information and does not require a spatially oriented motor response. Additionally, the two test types are balanced, such that in one condition participants are presented with a single location and four object choices (all from the studied set) and in the other condition participants are presented with

a single object and four location choices (all from the studied set). Thus, if the same effects are observed, we can be confident that the facilitation due to location overlap is not just an artifact of the original task design.

In the present study, we implemented the modified grid task as described above. Due to an experimenter error in the first experiment, we ran a second replication experiment. In both, we predicted that location overlap would facilitate new learning while object overlap would interfere with new learning, consistent with our previous findings. Critically, we predicted that these effects would be observed irrespective of the test type. This would suggest that the observed effects generalize across multiple response procedures and would strengthen the findings from the original task design.

Method

Participants

Experiment 1

Participants were recruited from the University of Oregon human subjects pool and received course credit for their participation. Informed consent was obtained from all participants, and experimental procedures were approved by Research Compliance Services at the University of Oregon. We recruited 51 online participants during the summer term (34 female, 16 male, 1 other), ages 18-27 years (M = 20.54, SD = 1.66). We recruited an additional 317 in-person participants during the subsequent terms (238 female, 66 male, 13 other), ages 18-27 years (M = 18.90, SD = 1.29). Consistent with past studies by the authors (Chaloupka & Zeithamova, 2024), we found that setting (in-person, online) did not affect the pattern of results so we combined the samples for all analyses. In total, we recruited 368 participants (272 female, 82 male, 14 other), ages 18-27 years (M = 19.12, SD = 1.46). The target sample size was

determined to be 320 (8 conditions, 40 per condition) based on a power analysis (α = .05, power = .80, partial η^2 = .025 estimated for each main effect). We excluded 10 participants for failing to pass the attention check and 9 participants for failing to score above chance on at least one of the grids. The remaining 349 participants were used in all analyses.

Experiment 2

Again, participants were recruited from the University of Oregon human subjects pool and received course credit for their participation. Informed consent was obtained from all participants, and experimental procedures were approved by Research Compliance Services at the University of Oregon. We recruited 234 in-person participants (169 female, 57 male, 8 other), ages 18-27 years (M = 19.02, SD = 1.29). For consistency with our prior experiments, the target sample size was 240 participants (6 conditions, 40 per condition). We excluded 11 participants for failing to pass the attention check and 4 participants for failing to score above chance on at least one of the grids. The remaining 219 participants were used in all analyses.

Procedure

Overview

In both experiments, participants completed a version of a grid learning task previously developed by the authors in which they learned grids of object-location associations (Chaloupka & Zeithamova, 2024). Each 8x8 grid contained eight objects in various locations throughout the grid (see Figure 2.1). Each participant sequentially learned two object-location grids, where the second grid would overlap with the first in the objects, locations, both, or neither. To require fewer participants, the full overlap condition was dropped for Experiment 2 since the effects of object overlap and location overlap never interact. The grid task was administered using PsychoPy (Peirce et al., 2019) for in-person participants and Pavlovia for online participants.

Stimuli

To create the grids used in both experiments, we started with 18 unaltered stimuli selected from the BOSS stimulus sets (Brodeur et al., 2010, 2014) used under the Creative Commons Attribution License (https://creativecommons.org/licenses/by-sa/3.0/). Two of these stimuli were selected to be used in the training phase. The remaining 16 stimuli were randomly split into two sets of eight. We created two sets of locations by pseudo-randomly selecting locations from the grid. We combined these two sets of locations and the two sets of stimuli to create eight distinct grids (two versions of each possible combination).

Participants were randomly assigned one of these grids to be their starting grid. Their second grid was chosen from the remaining grids based on the condition that the participant was randomly assigned to (see Figure 2.1). In the no overlap control group, the second grid used a new set of objects and a new set of locations. In the object overlap group, the second grid contained the same set of objects, but placed in a new set of locations. In the location overlap group, the second grid contained a new set of objects, but in the same locations as the first grid. In the full overlap group, the second grid used the same set of objects and the same set of locations, but the objects were shuffled so that the grids were not identical. This full overlap condition was only used in Experiment 1.

Grid Learning

In both experiments, participants first learned their starting grid (Grid 1). The grid learning procedure was the same for Grid 1 and Grid 2 (Figure 3.1). The grid was displayed on screen for 6 s followed by 4 s of a fixation cross. Two different test types were used, with half of participants assigned to each. For the first test type (Fig. 3.1A), a grid appeared on screen with four locations marked with ‘1’, ‘2’, ‘3’, and ‘4’. A single stimulus was displayed beneath the

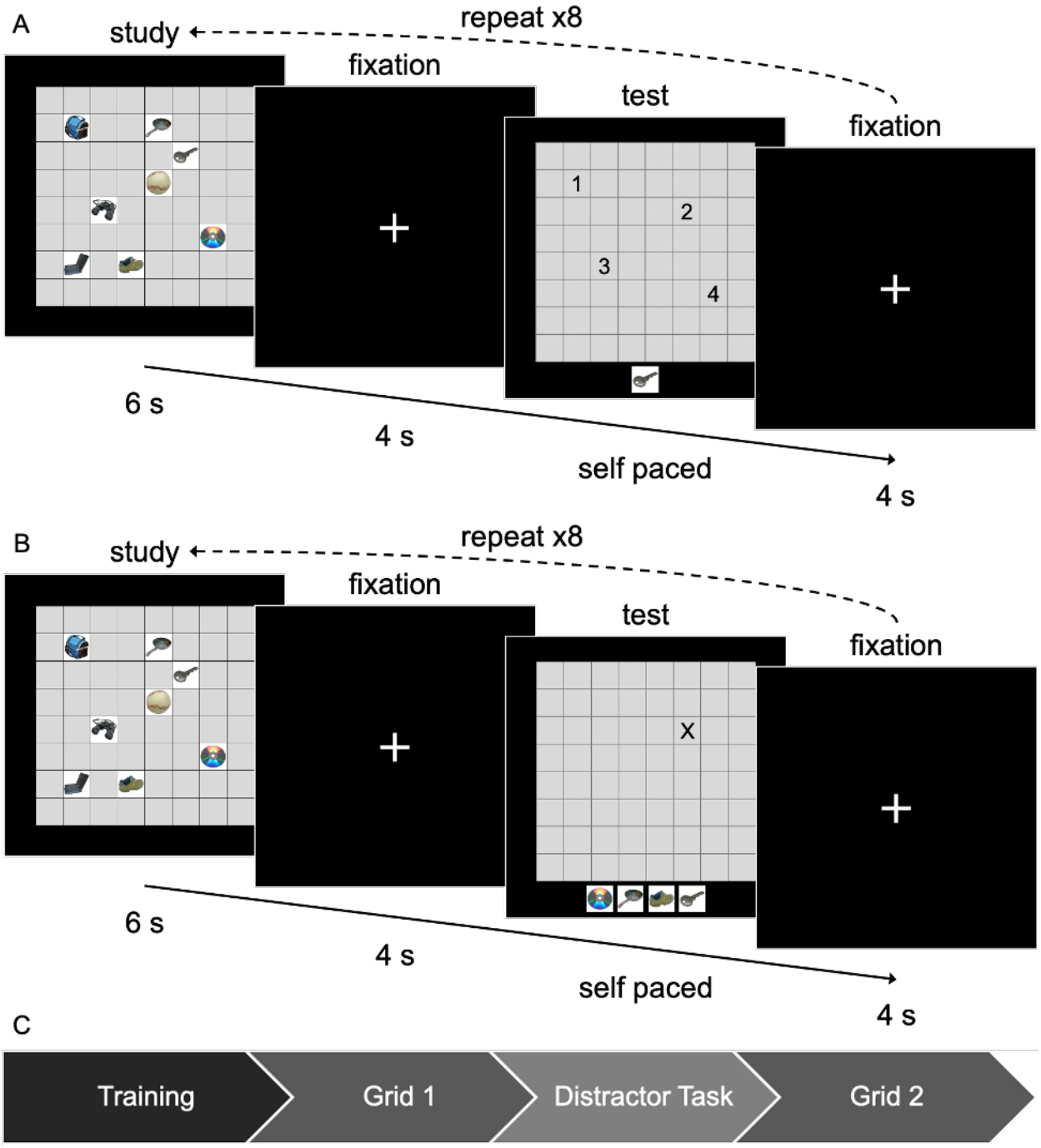

Figure 3.1. Overview of the grid learning task. (A) Half of participants learned each of the two grids using this process. During the test phase, they were shown one stimulus below the grid with four locations marked on the grid. (B) The other half of participants learned each of the two grids using this process. During the test phase, they were shown four stimuli below the grid with a single location marked on the grid. (C) Overview of the timeline of the grid task. Images used in this figure are unaltered images from the BOSS stimulus sets (Brodeur et al., 2010, 2014) used under the Creative Commons Attribution License (https://creativecommons.org/licenses/by-sa/3.0/).

grid, and the participant had to select which of the four marked locations the stimulus belonged to. The other three locations were also part of the same location set. For the second test type (Fig. 3.1B), a grid appeared on screen with a single location on the grid marked with an 'X'. Four stimuli were displayed beneath the grid, and the participant had to select which of the four stimuli belonged to the marked location in the grid. The other three stimuli were also part of the same stimulus set. For both test types, the test was self-paced, and participants did not receive feedback. The test probe was followed by 4 s of a fixation cross, marking the end of the trial. This process repeated for a total of eight trials. We recorded the proportion of correct trials out of eight for each participant. Participants who performed at or below chance (25%) were categorized as 'non-learners' and excluded from analysis. Prior to the actual task, participants received instructions and practiced the task using a simplified training grid with the two training stimuli.

Math Distractor Task

In both experiments, participants next completed a math distractor task. On each trial, participants were shown a simple arithmetic expression and asked to evaluate if the expression was true or false using the 'T' and 'F' keys, respectively. For example, "3 + 5 = 9" required a response of 'F'. Each arithmetic problem was displayed on screen for 4 s during which participants made their response. They then received feedback on screen for 2 s indicating if they were correct, incorrect, or too slow to respond. Participants completed 20 trials for a total of 2 min. This served as an attention check and working memory flush, preventing participants from actively rehearsing the previously learned grid. To ensure engagement, participants with less that 75% accuracy on this task were excluded from analyses.

Second Grid Learning

Following the math distractor task, participants learned their second grid using the same procedure as the first. In Experiment 1, participants were randomly assigned to one of eight groups using a 2x2x2 design (object overlap [different set of objects vs. same set of objects] x location overlap [different set of locations vs. same set of locations] x test type [single object probe vs. single location probe]; see Figure 2.1). In Experiment 2, participants were randomly assigned to one of six groups. By dropping the full overlap condition, we used a 3x2 design (overlap type [no overlap vs. object overlap vs. location overlap] x test type [single object probe vs. single location probe]. In addition to recording the proportion of correct trials for Grid 2, we also calculated a difference score by subtracting the proportion of correct trials for the first grid from the proportion of correct trials for the second grid (Grid 2 minus Grid 1). Thus, a difference score of 0 indicated that their memory for the two grids was equivalent, a positive score meant that they performed better on the second grid (indicative of facilitation), and a negative score indicated that they performed better on the first grid (indicative of proactive interference).

Results

Experiment 1

First, we measured the proportion correct on Grid 1 (M = .84, SD = .15). Since this grid was learned prior to any manipulation, we predicted no significant differences between groups. To test this, we ran a 2x2x2 factorial ANOVA with the proportion correct on Grid 1 as the dependent variable (Figure 3.2A). We found a significant main effect of object overlap, $F(1, 341) = 4.16$, $p = .042$, $\eta_p^2 = .01$, a significant main effect of location overlap, $F(1, 341) = 8.34$, $p = .004$, $\eta_p^2 = .02$, and a significant main effect of test type, $F(1, 341) = 5.29$, $p = .022$, $\eta_p^2 = .02$. No interactions were significant (all p's > .10). Due to an experimenter error, the randomization

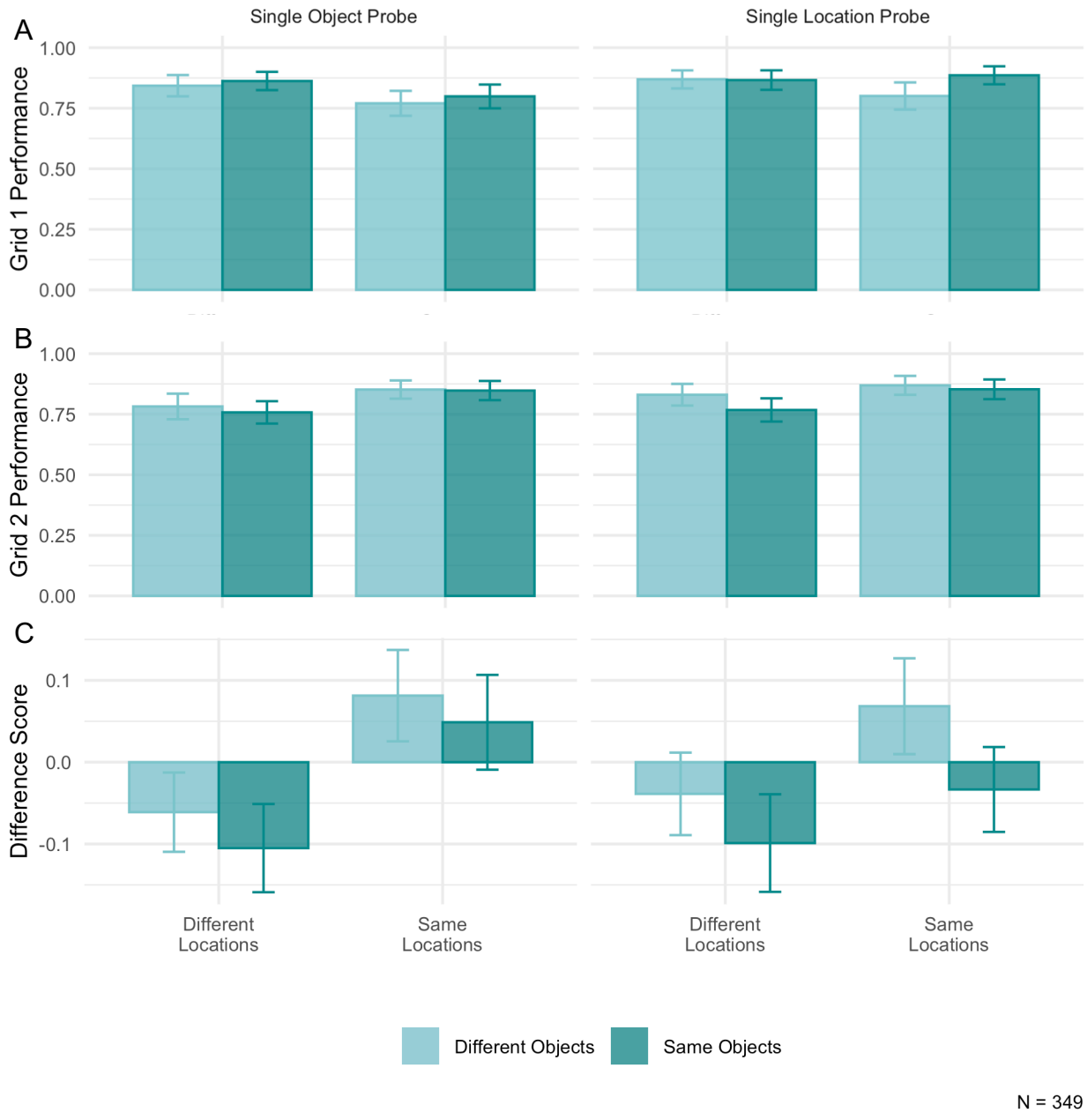

Figure 3.2. Experiment 1 results. (A) The *y*-axis is the proportion of correct trials on the first grid. There was a main effect of object overlap ($p = .042$), a main effect of location overlap ($p = .004$), and a main effect of test type ($p = .022$). (B) The *y*-axis is the proportion of correct trials on the second grid. There was a main effect of location overlap ($p < .001$), and a trending effect of object overlap ($p = .092$). (C) The *y*-axis is the difference score calculated by subtracting the proportion of correct trials for the first grid from the proportion of correct trials for the second grid (Grid 2 minus Grid 1). A positive number indicates improved performance on the second grid. There was a main effect of object overlap ($p = .003$) and a main effect of location overlap ($p < .001$). Error bars represent 95% confidence intervals for all plots.

in the condition files was incorrect. This led to an imbalance in difficulty for the first grid, leading to differences in performance prior to any experimental manipulation. This error prompted us to run Experiment 2, a replication study with the correct condition files.

Next, we measured the proportion correct on Grid 2 (M = .82, SD = .15). To test this, we ran a 2x2x2 factorial ANOVA with the proportion correct on Grid 2 as the dependent variable (Figure 3.2B). We found a significant main effect of location overlap, $F(1, 341) = 19.83$, $p < .001$, $\eta_p^2 = .05$, driven by better performance when locations overlapped (M = .86, SD = .13) compared to when locations did not overlap (M = .78, SD = .16). We also found a trending main effect of object overlap, $F(1, 341) = 2.86$, $p = .092$, $\eta_p^2 = .01$, driven by better performance when objects did not overlap (M = .83, SD = .15) compared to when objects overlapped (M = .80, SD = .16). No other effects were significant (all p's > .20).

To account for individual differences in grid learning, we used the difference score (proportion correct for Grid 2 minus proportion correct for Grid 1; M = -.02, SD = .20) for our main analysis. To determine the effects of object overlap, location overlap, and test type on task performance, we ran a 2x2x2 factorial ANOVA with the difference score as the dependent variable (Figure 3.2C). Consistent with our hypothesis, we found a significant main effect of object overlap, $F(1, 341) = 9.09$, $p = .003$, $\eta_p^2 = .03$, driven by increased performance when objects did not overlap (M = .01, SD = .19) compared to when objects overlapped (M = -.05, SD = .20). In line with our hypothesis, we also found a significant main effect of location overlap, $F(1, 341) = 35.13$, $p < .001$, $\eta_p^2 = .09$, driven by increased performance when locations overlapped (M = .04, SD = .19) compared to when locations did not overlap (M = -.08, SD = .18). Critically, we found no interaction between test type and object overlap, $F(1, 341) = 1.16$, $p = .281$, $\eta_p^2 = .00$, and no interaction between test type and location overlap, $F(1, 341) = 2.44$, $p =$

.119, η_p^2 = .01, indicating that the observed main effects are not dependent on the test type. No other comparisons were significant (all *p*'s > .40). While this main analysis of difference scores showed the expected effects, it is not possible to rule out that item effects may have played some role in the results given the error in the condition files. Thus, we aimed to replicate the findings in a second experiment after correcting the error.

Experiment 2

First, we measured the proportion correct on Grid 1 (*M* = .88, *SD* = .12). Since this grid was learned prior to any manipulation, we predicted no significant differences between groups. To test this, we ran a 3x2 factorial ANOVA with the proportion correct on Grid 1 as the dependent variable (Figure 3.3A). We found a trending main effect of test type, $F(1, 213) = 3.14$, $p = .078$, $\eta_p^2 = .01$, driven by slightly better performance with the single location probe (*M* = .90, *SD* = .12) than with the single object probe (*M* = .87, *SD* = .12). We found no main effect of overlap, $F(2, 213) = 0.64$, $p = .529$, $\eta_p^2 = .01$, and no interaction, $F(2, 213) = 0.08$, $p = .920$, $\eta_p^2 = .00$. While there was a marginal difference in performance based on test type, we critically saw no differences due to overlap prior to manipulation.

Next, we measured the proportion correct on Grid 2 (*M* = .87, *SD* = .15). To test this, we ran a 3x2 factorial ANOVA with the proportion correct on Grid 2 as the dependent variable (Figure 3.3B). We found no main effect of overlap, $F(2, 213) = 2.16$, $p = .118$, $\eta_p^2 = .02$, no main effect of test type, $F(1, 213) = 0.72$, $p = .396$, $\eta_p^2 = .00$, and no interaction, $F(2, 213) = 1.52$, $p = .222$, $\eta_p^2 = .01$. This is contrary to our hypothesis, which predicted that the type of overlap would affect performance on the second grid.

To account for individual differences in grid learning, we again used the difference score (proportion correct for Grid 2 minus proportion correct for Grid 1; *M* = -.02, *SD* = .17) for our

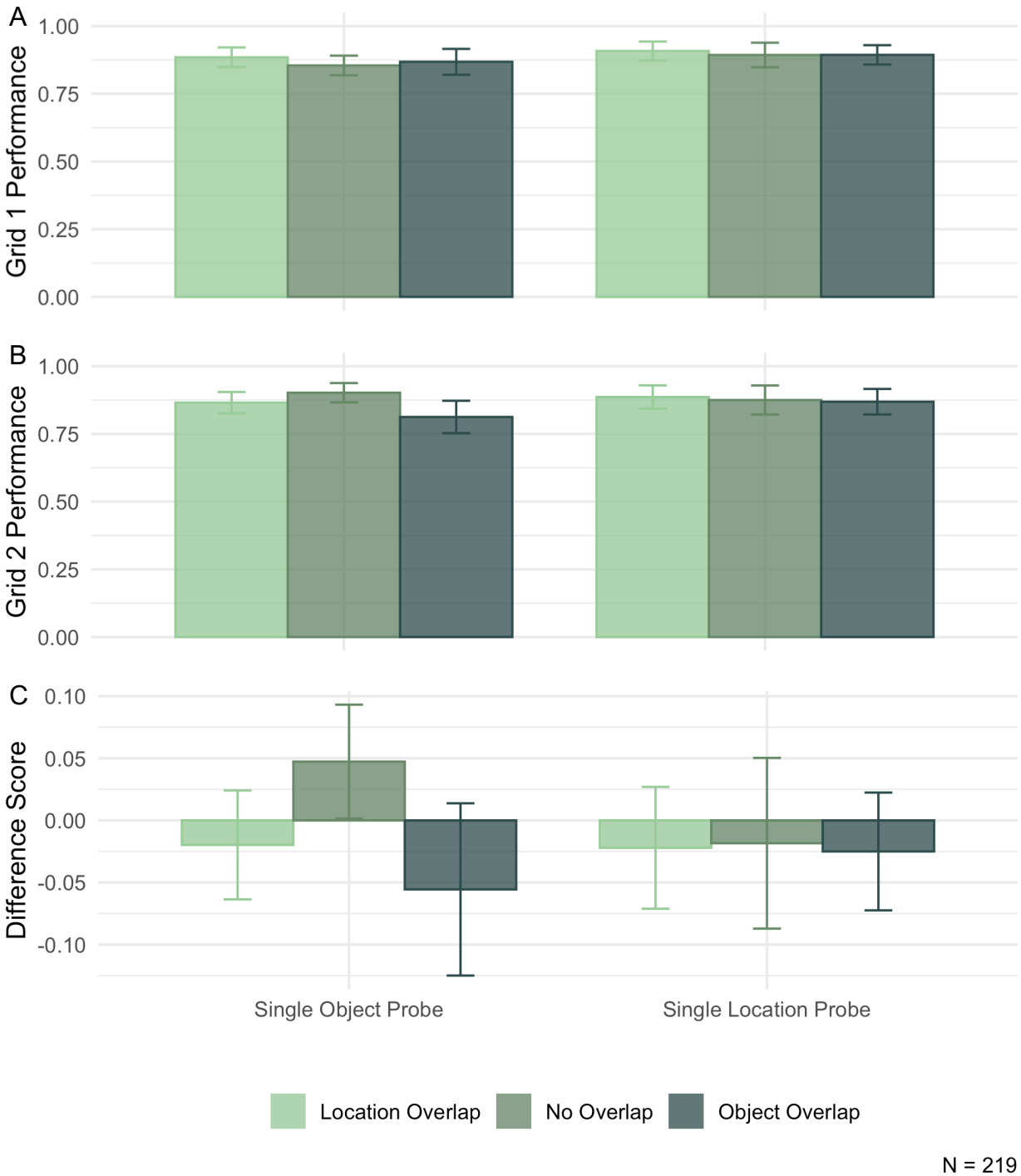

Figure 3.3. Experiment 2 results. (A) The *y*-axis is the proportion of correct trials on the first grid. There were no significant effects. (B) The *y*-axis is the proportion of correct trials on the second grid. There were no significant effects. (C) The *y*-axis is the difference score calculated by subtracting the proportion of correct trials for the first grid from the proportion of correct trials for the second grid (Grid 2 minus Grid 1). A positive number indicates improved performance on the second grid. There were no significant effects. Error bars represent 95% confidence intervals for all plots.

main analysis. To determine the effects of overlap and test type on task performance, we ran a 3x2 factorial ANOVA with the difference score as the dependent variable (Figure 3.3C). We found no main effect of overlap, $F(2, 213) = 1.99$, $p = .139$, $\eta_p^2 = .02$, no main effect of test type , $F(1, 213) = 0.30$, $p = .583$, $\eta_p^2 = .00$, and no interaction, $F(2, 213) = 1.54$, $p = .216$, $\eta_p^2 = .01$. Post hoc comparisons using the Tukey HSD test revealed no significant comparisons, although performance in the no overlap condition was numerically better than both the location overlap condition, $t(213) = 1.26$, $p = .421$, and the object overlap condition, $t(213) = 1.97$, $p = .121$. While we did not expect to find a main effect of test type or an interaction, the lack of effect of overlap was contrary to our hypothesis.

Further inspection revealed that the lack of an effect of overlap may have been due to a ceiling effect. The average performance on both grids was several percentage points higher than in Experiment 1. In fact, 86 participants (39%) had a perfect score on Grid 1, 89 participants (41%) had a perfect score on Grid 2, and 40 participants (18%) had a perfect score on both grids. While we did not collect the full target sample size, the lack of effect of overlap is more likely due to this ceiling effect than to the experiment being underpowered. A Shapiro-Wilk test of normality revealed that neither performance on Grid 1, $W = .82$, $p < .001$, or Grid 2, $W = .81$, $p < .001$, were normally distributed.

Discussion

Here, we used a modified version of the grid task to determine if the facilitatory effect of location overlap and interference effect of object overlap generalize across multiple response procedures. In Experiment 1, we replicated results from Chapter 2, finding that location overlap led to increased performance and object overlap led to decreased performance. Critically, we found no interactions with test type, such that the pattern of results was the same regardless of

which test type was used. This suggests that these effects of overlap extend beyond a spatially oriented response procedure, reinforcing the findings from the original task design. While these findings are highly encouraging, we must take them with caution. Due to an error by the experimenter, the randomization in the condition files was incorrect. This led to an imbalance in difficulty for the first grid, prior to any experimental manipulation. Thus, we ran a second experiment to try to replicate these findings.

In Experiment 2, we failed to support our hypothesis, finding no main effects and no interaction. The lack of an effect of overlap is in contrast to our previous findings. Interestingly, participants scored better on both grids than in previous versions. This created a ceiling effect, as well over half of participants (61%) had a perfect score on at least one of the two grids. We did not reach the target sample size for this experiment to achieve the desired statistical power, but we weren't short by much. Thus, the ceiling effect is a more likely explanation for the lack of an effect than the lack of power.

While the findings in Experiment 1 replicate our results from Chapter 2, the findings from Experiment 2 cast some doubt on the generalizability of these effects. Although the results of the current experiments were mixed, further work suggests that the drag-and-drop procedure is not necessary to observe the effects of overlap. In Chapter 4, we present two pilot samples that use a similar response procedure to the single object probe test type. While not an identical procedure, it similarly avoids placing emphasis on the spatial information. In both pilot samples, we observe a facilitation effect due to location overlap and interference due to object overlap. These findings replicate the results from Chapter 2 as well as Experiment 1 reported here, strengthening our claim that the differential effects of overlap extend across response procedures.

In the experiments described in this chapter, we learned that the modified experimental design has its flaws. To improve this design, the task needs to be constructed in such a way as to avoid ceiling effects, allowing for a normally distributed dependent variable. One solution would be to decrease the presentation of the grid during the study phase, but too short of a presentation duration may lead to suboptimal encoding strategies, such as only focusing on two or three objects at a time. In this case, the memory probe would be more a matter of luck. If the probed object or location was one of the two or three studied, the participant would get the trial correct even if they were far from learning the entire grid. Perhaps the best solution would be to increase the number of objects on the grid. This would make learning the grid more difficult, eliminating the ceiling effect. Future work is needed to determine the best version of this modified task.

One glaring limitation of the modified grid task is the use of memory probes that only test a single object-location association at a time. Based on our interpretation of our original findings, the facilitatory effect of location overlap is due to a form of memory generalization, potentially a spatial schema. This means that the facilitation comes from learning the entire grid, not just managing to remember one specific object-location association from the grid. Thus, while the modified version of the task alleviates some of the original concerns, it introduces others. By only probing one association at a time, we fail to accurately capture the learning rate of the entire grid. In the original version of the task, counting the number of trials to learn the whole grid was an effective way of measuring the rate of learning. One potential solution would be to include a bank of objects that matched the number of possible locations. Assuming that participants are able to figure out that the outside edge of the grid is never used, a bank of 36 objects would provide a balanced response, addressing one of the original concerns.

Another potential solution could be to alter the response procedure slightly. Participants could use the arrow keys to navigate to different squares on the blank grid. After selecting the square of their choosing, they could use the mouse to click on one of the objects from the object bank, filling in the grid with each selection. This would enable a full reconstruction of the grid while eliminating the spatially oriented motor response of dragging an object to a specific location on the grid. Perhaps a future study could implement this response procedure coupled with a larger object bank to balance the choices. This would have the potential to alleviate the original concerns while still allowing for a full reconstruction of the grid.

In summary, despite the lingering concerns due to the respective shortcomings of the two experiments reported here, we remain optimistic regarding the opposing effects of location overlap and object overlap. Even with an experimenter error, we did manage to replicate our past findings in Experiment 1. We found that location overlap caused facilitation while object overlap caused interference, and that these effects were observed irrespective of test type. While future work is needed to confirm these findings, the results reported here partially support our past findings. They also inform future work by highlighting limitations with the current experimental design. Finally, we discussed potential solutions to these limitations and paved the way for future work to replicate and expand upon our findings.

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CHAPTER IV

THE ROLE OF THE MEDIAL TEMPORAL LOBE AND HIPPOCAMPUS IN FACILITATION AND INTERFERENCE

The cognitive neuroscience of memory has fascinated researchers for decades, yet many related lines of work have proceeded largely in parallel. This has led to two well-established yet seemingly conflicting findings: that overlapping experiences facilitate new learning in some cases while causing interference in others. Facilitation may occur through the formation and instantiation of complex mental representations, known as schemas (Attneave, 1957; Bartlett, 1932; King et al., 2019; Posner et al., 1967; Sommer, 2016; Tompary et al., 2020; van Kesteren et al., 2014). In particular, spatial schemas seem especially facilitatory for new learning (Guo & Yang, 2020; Kyle et al., 2015; Tse et al., 2007; van Buuren et al., 2014). Collectively, this substantial body of work suggests that learning and memory are aided by overlapping events.

In contrast, overlapping experiences can hinder new learning via memory interference (Bunting, 2006; Dallet & Wilcox, 1968; Goggin & Wickens, 1971; Keppel & Underwood, 1962; Maslow, 1934; Melton & von Lackum, 1941; Underwood, 1957; Wickens et al., 1963; Wixted & Rohrer, 1993). These studies suggest that overlapping events create competition, leading to either proactive interference – when previous memories hinder new learning – or retroactive interference – when newly learned information leads to forgetting of previous memories. Research has demonstrated that interference affects associative memory as well (Kliegl & Bäuml, 2021; Postman et al., 1974; Tulving & Watkins, 1974). This informs us that overlapping events can hinder our ability to link information together, beyond memory for individual items.

Despite the parallels between these lines of work, only recently have researchers started examining facilitation and interference together (W. R. Cox et al., 2021; Dimsdale-Zucker et al.,

2018; Molitor et al., 2021). However, research that simultaneously studies facilitation and interference *both as an outcome of overlap* is scarce. In Chapter II, we found that both facilitation and interference can result from two different types of overlap (Chaloupka & Zeithamova, 2024). Using a novel object-location association grid task, overlapping locations facilitated new learning while overlapping objects led to interference. While this successfully links the two behavioral phenomena into a single study, we have yet to uncover the full picture of how the brain supports learning when events overlap in different ways.

After Tse and colleagues' (2007) landmark study, researchers began investigating the neural underpinnings of schemas. While the shift from the medial temporal lobe (MTL) to neocortex during learning was previously known, the involvement of the ventromedial prefrontal cortex (vmPFC) in schema-related learning was first detailed by van Kesteren and colleagues (2012). This finding, along with an emphasis on the role of the hippocampus, was later confirmed (Gilboa & Marlatte, 2017). The interplay of the vmPFC, MTL, and hippocampus has also been identified as key to memory generalization more broadly (Bowman & Zeithamova, 2018; Robin & Moscovitch, 2017; Schlichting et al., 2015; Shohamy & Wagner, 2008; Zeithamova & Preston, 2010). Memory generalization can be defined as leveraging prior knowledge to make predictions in novel situations, and schemas are an exemplar of this.

While research on schemas has focused primarily on hippocampal-cortical interactions, an adjacent line of work has investigated neural memory integration – the process by which overlapping events evoke more similar, or integrated, patterns of neural activity in specific brain regions. This is one potential mechanism that underlies successful memory generalization. This line of research has examined hippocampal subfields, identifying the CA_1 (cornu ammonis 1) as

a site of neural memory integration (Schlichting et al., 2014; Schlichting & Preston, 2015; Takeuchi et al., 2022). CA_1's involvement in schema formation remains an open question.

When it comes to interference, the question isn't so much how the brain *supports* interference, but rather how the brain *mitigates* interference. In contrast to neural memory integration, a leading theory suggests that overlapping events are actually represented as orthogonal as a way to keep competing memories more distinct. This process is known as neural pattern separation. In some cases, neural representations of highly similar stimuli become negatively correlated via pattern differentiation or repulsion. Studies in both rodents and humans have identified the hippocampal subfields CA_3 and dentate gyrus (DG) as brain regions in which these phenomena occur (Bakker et al., 2008; Chanales et al., 2017; Favila et al., 2016; Leutgeb et al., 2007; Yassa & Stark, 2011). While this is a fascinating finding, our understanding of when overlapping experiences lead to pattern separation as a mechanism for mitigating interference versus integration as a mechanism of facilitation remains incomplete.

In the present study, we used a within-subjects design of an object-location association grid task developed by the authors (Chaloupka & Zeithamova, 2024). In combination with high-resolution functional magnetic resonance imaging (fMRI), we investigated how the brain supports facilitation and mitigates interference when different types of information overlap. First, we tested whether certain brain regions were preferentially active during the object overlap condition versus the location overlap condition. The perirhinal cortex (PRC) is known for object recognition (Bartko et al., 2007b, 2007a; Miyashita, 2019; Tamura et al., 2017), so we predicted that the PRC would be more active during the object overlap condition. The parahippocampal cortex (PHC) is known for spatial processing (Epstein & Baker, 2019; Epstein & Kanwisher, 1998; Sun et al., 2021), so we predicted that the PHC would be more active during the location

overlap condition. Given its role in schema formation and memory generalization, we also predicted that the vmPFC would be more active during the location overlap condition. Additionally, we utilized pattern similarity analysis to test whether certain cortical regions and hippocampal subfields demonstrated neural memory integration or pattern separation. We predicted that PHC, vmPFC, and CA_1 would integrate grids with overlapping locations, PRC would integrate grids with overlapping objects, and $CA_{2/3}$, and DG would pattern separate grids with overlapping objects. Finally, we predicted that greater levels of integration in cortical regions and CA_1 would lead to greater facilitation, while greater levels of pattern separation in $CA_{2/3}$ and DG would lead to less interference.

Method

Participants

Participants were recruited from the University of Oregon and received financial compensation for their participation. All participants provided written informed consent, and experimental procedures were approved by Research Compliance Services at the University of Oregon. Additionally, participants were right-handed, native English speakers, and underwent screening for metal implants, neurological conditions, and medications that may affect brain function or pose a risk in the MRI scanner. In total, 24 participants were recruited. Three participants were excluded from analyses due to incomplete data or inability to finish the task. The remaining 21 participants were used in all analyses (12 female, 8 male, and 1 other), age 18-29 years (M = 19.52, SD = 2.38).

Procedure

Overview

Participants came into the lab where they provided consent, completed an MRI screening form, and provided demographic information. Next, they completed a training task to familiarize them with the task they would complete in the scanner, a version of the grid learning task first developed by the authors in which they learned grids of object-location associations (Chaloupka & Zeithamova, 2024). Upon completion of this training task, participants were escorted to the imaging center where they were further screened by the MRI technician, including the use of a ferromagnetic detector. Once in the scanner, a T1-weighted (T1w) anatomical scan was collected while participants had no task to complete. Next, two functional scans were collected while participants completed the main grid task. Following this, participants viewed a slideshow of pictures taken by the author of nature scenes from around Oregon as a break from the task while a T2-weighted (T2w) anatomical scan was collected. Finally, two more functional scans were collected while participants completed the main grid task. After being removed from the scanner, participants were debriefed, compensated, and given pictures of their brain. Both the training task and main grid task were administered using PsychoPy (Peirce et al., 2019).

Stimuli

To create the grids used in this study, we selected 18 unaltered stimuli from the BOSS sets (Brodeur et al., 2010, 2014) used under the Creative Commons Attribution License (https://creativecommons.org/licenses/by-sa/3.0/). Two of these stimuli were randomly selected to be used in the training phase. The remaining 16 stimuli were randomly split into two sets of eight. We created two sets of eight locations each, pseudo-randomly selected from the grid, with the constraints that no location had a side on the edge of the grid, and no two locations shared a

side with each other. We combined these two sets of objects and two sets of locations to create eight distinct grids (two versions of each possible combination; Figure 4.1). Participants were randomly assigned one of the grids to be their base grid. We also created a training grid with two objects placed in locations that were not used in either of the location sets in the main grids.

Grid Learning Task

Training Task. First, participants completed a training task outside of the scanner. At the beginning of the training task, participants were trained on the mechanics of the task using the simplified training grid. Then, they learned their base grid. After studying the grid for 6 s followed by a fixation cross for 4 s, participants attempted to recreate the grid by dragging and dropping each object to its location on the grid, as in the version of the task described in Chapter II (Chaloupka & Zeithamova, 2024). All participants completed eight trials during the training phase, regardless of performance.

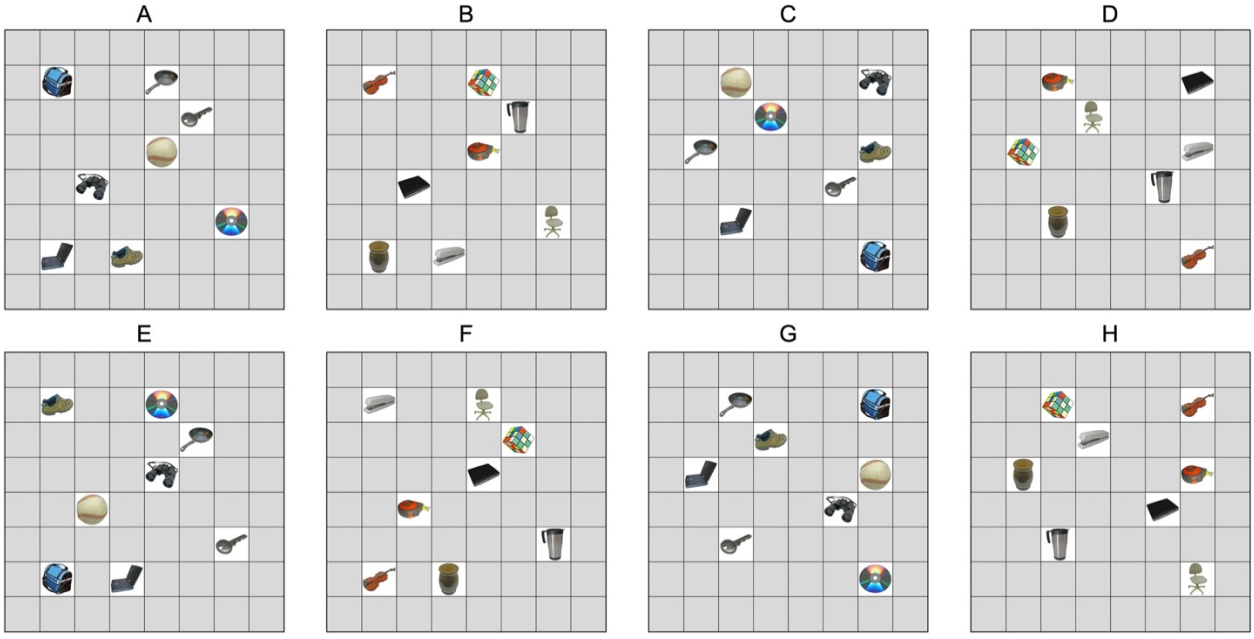

Figure 4.1. Stimulus grids. Participant were randomly assigned one of the grids as their base grid. If this grid was from the top row, their four experimental grids were all the grids from the bottom row, and vice versa. For example, if a participant was assigned grid A as their base grid, the no overlap condition would be grid H, the object overlap condition would be grid G, the location overlap condition would be grid F, and the full overlap condition would be grid E.

Next, participants were trained on an odd/even distractor task. On each trial, they had to identify whether a number between 1 and 40 presented on screen for 2 s was odd or even. They completed four trials where feedback was presented on screen for 1 s, and 10 additional trials where a fixation cross was presented in place of feedback.

Finally, participants completed another eight trials of the grid task, this time with an altered response procedure to match how they would respond while in the scanner. The base grid was presented on screen for 6 s followed by a jittered fixation cross (2-6 s). Instead of recreating the entire grid, participants were shown a memory probe for 4 s with four locations marked on an otherwise blank grid and one of the eight objects they had just studied at the bottom of the screen (Figure 4.2A). They had to identify which of the four locations contained the object within the 4 s. The four marked locations were pseudo-randomly selected such that one of them was the correct location, one of them was from the same location set, one was from the other location set not used in the base grid, and the last location belonged to neither location set. Following the memory probe, another jittered fixation cross (2-6 s) was presented during the inter-trial interval.

Main Task. Once inside the scanner, participants completed the main grid task during each of the four functional scans (Figure 4.2). The task used a within-subjects 2x2 design (object overlap [different set of objects vs. same set of objects] x location overlap [different set of locations vs. same set of locations]). Within each run, participants alternated between blocks of four trials of the odd/even task and blocks of the grid task (Figure 4.2B). To buffer the start of each run, participants first completed two trials of the odd/even task. Then, they completed one base grid block before moving on to the first experimental grid block. The order of experimental grid blocks was counterbalanced across runs, and base grid blocks were interleaved with the experimental grid blocks to reinforce the base grid prior to each manipulation. Within each grid

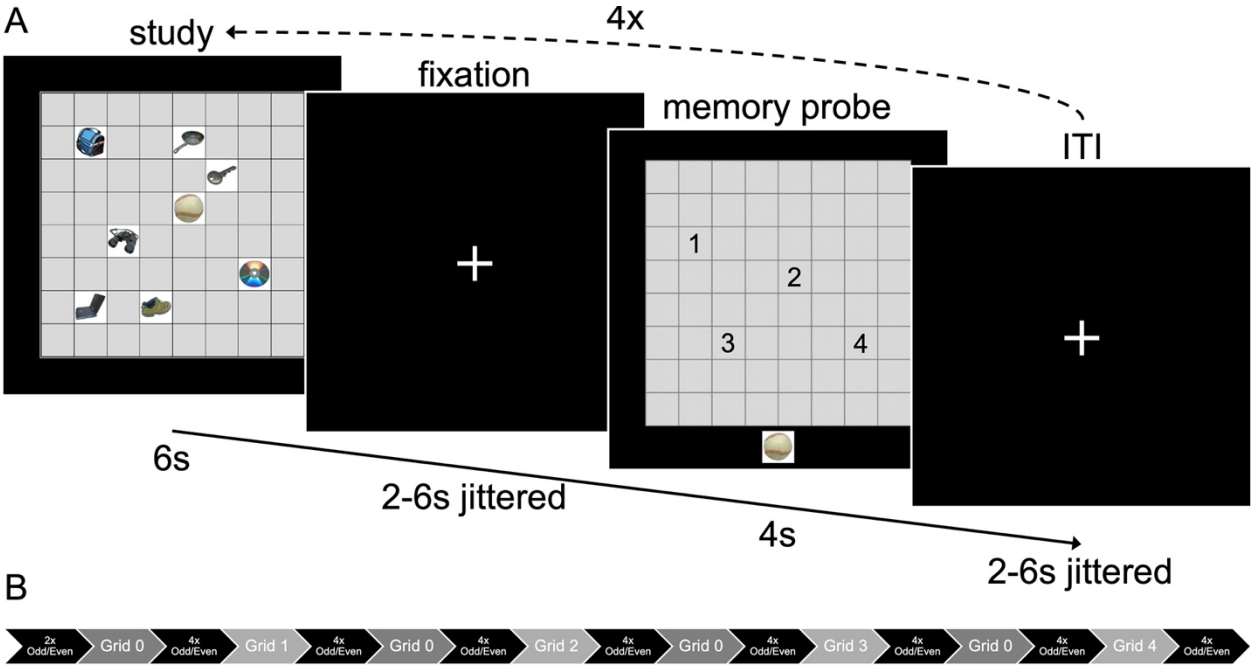

Figure 4.2. Task design. (A) The memory probe procedure used to test grid learning in the main grid task during the functional runs. (B) Overview of the timeline for each of the four functional runs. Grid 0 represents the base grid. The order of the experimental grids (grids 1-4) was counterbalanced across runs.

block, participants completed four trials of the grid task with the memory probe response procedure used in the final phase of the training task (Figure 4.2A). After studying the grid for 6 s followed by a jittered fixation cross (2-6 s), participants were shown a memory probe with four locations marked on the grid. They responded using a right-hand button box with their index, middle, ring, and pinky fingers corresponding to the four possible options. Proportion of correct responses on the memory probe trials was used as the behavioral measure.

fMRI Acquisition

We used a Siemens 3T Skyra MRI system to collect all images. We collected an anatomical image using a T1w MPRAGE sequence: TR = 2.5 s, TE = 3.43 ms, flip angle = 7°, FOV = 256 mm, 1 mm isotropic voxels, duration = 5:59. An additional anatomical image was collected using a T2w sequence: TR = 13.52 s, TE = 88 ms, flip angle = 150°, FOV = 220 mm,

voxel size = .4 mm x .4 mm x 2 mm, 65 coronal slices, duration = 7:01. The T2w image was used for hippocampal subfield segmentation. Four functional images were collected with a gradient-echo echo-planar imaging (EPI) pulse sequence: TR = 2 s, TE = 28.4 ms, flip angle = 90°, FOV = 207 mm, 81 oblique axial slices, voxel size = 1.78 mm x 1.78 mm x 1.8 mm, GRAPPA factor 2, multiband factor 3, duration = 12:30. All raw dicom images were converted to Brain Imaging Data Structure (BIDS) format using Dcm2Bids (Boré et al., 2023).

fMRI Preprocessing

Results included in this manuscript come from preprocessing performed using fMRIPrep 23.1.4 (Esteban et al., 2019, 2023), which is based on Nipype 1.8.6 (Esteban et al., 2022; Gorgolewski et al., 2011).

Preprocessing of B0 Inhomogeneity Mappings

A B0-nonuniformity map (or fieldmap) was estimated based on two echo-planar imaging (EPI) references with topup (Andersson et al., 2003).

Anatomical Data Preprocessing

The T1w image was corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al., 2010), distributed with ANTs (Avants et al., 2008), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using fast (FSL 5.0.10, Zhang et al., 2001). Brain surfaces were reconstructed using recon-all (FreeSurfer 7.3.2, Dale et al., 1999), and the brain mask estimated previously was refined with a custom

variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (Klein et al., 2017).

Functional Data Preprocessing

For each of the 4 BOLD runs per subject, the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated by aligning and averaging one single-band reference (SBRef). Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 5.0.10, Jenkinson et al., 2002). The estimated fieldmap was then aligned with rigid-registration to the target EPI reference run. The field coefficients were mapped on to the reference EPI using the transform. BOLD runs were slice-time corrected to 0.954 s (0.5 of slice acquisition range 0 s – 1.91 s) using 3dTshift (AFNI, Cox & Hyde, 1997). The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer 7.3.2) which implements boundary-based registration (Greve & Fischl, 2009). Co-registration was configured with six degrees of freedom. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions, Power et al., 2014) and Jenkinson (relative root mean square displacement between affines, Jenkinson et al., 2002). FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by Power et al. 2014). The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor, Behzadi et al., 2007).

Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with 128 s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 2% variable voxels within the brain mask. For aCompCor, three probabilistic masks (CSF, WM, and combined CSF+WM) are generated in anatomical space. The implementation differs from that of Behzadi et al. in that instead of eroding the masks by 2 pixels on BOLD space, a mask of pixels that likely contain a volume fraction of GM is subtracted from the aCompCor masks. This mask is obtained by dilating a GM mask extracted from the FreeSurfer's aseg segmentation, and it ensures components are not extracted from voxels containing a minimal fraction of GM. Finally, these masks are resampled into BOLD space and binarized by thresholding at 0.99 (as in the original implementation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (Satterthwaite et al., 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. Additional nuisance timeseries are calculated by means of principal components analysis of the signal found within a thin band (crown) of voxels around the edge of the brain, as proposed by Patriat et al. (2017).

Regions of Interest (ROIs)

We used the T2w image to segment the hippocampus into its subfields using segmentHA_T2 (FreeSurfer 7.4.1, Iglesias et al., 2015). These segmentations were converted to NIfTI with mri_convert (FreeSurfer 7.4.1) and co-registered to the T1w-reference using antsApplyTransforms (ANTs). The whole brain segmentations and the hippocampal subfield segmentations were then used to create bilateral ROI masks for each subject in native (T1) space.

We determined two sets of ROIs a priori. First, we used a set of hippocampal subfield ROIs (Figure 4.3A): CA_1, $CA_{2/3}$, CA_4, dentate gyrus (DG), and subiculum. CA_1 is involved in pattern integration (Schlichting et al., 2014; Schlichting & Preston, 2015) while $CA_{2/3}$ and DG have been implicated in pattern separation or differentiation (Bakker et al., 2008; Chanales et al., 2017; Favila et al., 2016; Leutgeb et al., 2007; Yassa & Stark, 2011). The second set of ROIs consisted of the whole hippocampus and several cortical ROIs (Figure 4.3B): perirhinal cortex (PRC), parahippocampal cortex (PHC), ventromedial prefrontal cortex (vmPFC), and lateral

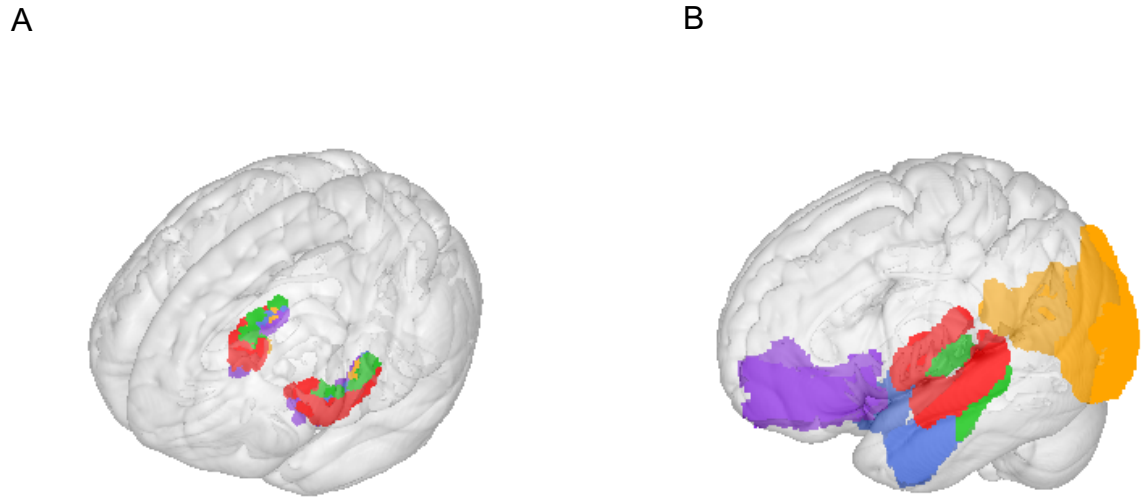

Figure 4.3. ROI masks from an example subject. (A) The hippocampal subfields: CA_1 in red, $CA_{2/3}$ in green, CA_4 in blue, DG in orange, and subiculum in purple. (B) Cortical ROIs: hippocampus in red, PHC in green , PRC in blue, LO in orange, and vmPFC in purple.

occipital cortex (LO). The PRC has been implicated in object recognition (Bartko et al., 2007b, 2007a; Miyashita, 2019; Tamura et al., 2017) and thus may be more sensitive to the object overlap condition. The PHC is involved in spatial processing (Epstein & Baker, 2019; Epstein & Kanwisher, 1998; Sun et al., 2021) and may be more sensitive to the location overlap condition. The vmPFC is involved in schema formation (Gilboa & Marlatte, 2017; Robin & Moscovitch, 2017; van Kesteren et al., 2012), so it may also be more sensitive to the location overlap condition where overlap creates facilitation. LO was included due to its role in the visual processing stream, and the hippocampus due to its role in learning and memory. Both sets of ROIs were used for the univariate analyses and the pattern similarity analyses.

Modelling fMRI Data

First-level models were carried out with the fMRI Expert Analysis Tool (FEAT, from FSL 5.0.10). Each run for each subject was modeled separately. Preprocessed BOLD images in each subject's native space were the inputs to the models. Images were high-pass filtered with a cutoff of 144 s and minimally smoothed using a 3 mm full width at half maximum Gaussian kernel. Custom explanatory variables (EVs) were used that modeled the display periods for the base grid and each of the four experimental grids, and separately modeled the corresponding memory probe periods, for a total of 10 EVs. Temporal derivatives of all 10 EVs were included in the models as well, along with six confound EVs representing the three dimensions of movement and three axes of rotation. Thus, a total of 26 parameter estimates (PEs) were obtained from the models. EVs were convolved with the canonical hemodynamic response function. The primary contrast of parameter estimates (COPE) included in the models contrasted the object overlap condition and the location overlap condition. An additional task vs. baseline COPE was obtained.

Univariate Analyses

To mirror the behavioral analysis, we conducted a 2x2 (object overlap x location overlap) repeated measures ANOVA with the PEs as the dependent variable. Additionally, we analyzed the primary contrast that compared the object overlap condition to the location overlap condition. Averaged contrast estimates for each participant and for each ROI were calculated from the *z*-statistic COPEs using fslmeants (FSL 5.0.10) while applying the bilateral ROI masks. The *z*-statistic COPEs were used instead of the raw COPEs for easier interpretation of the results. A one-sample *t*-test was run for each ROI to determine if the group average contrast estimate significantly differed from zero. As a sanity check, the same analysis was conducted on the task vs. baseline contrast, where the grids and memory probes were modeled as part of the task while the fixation crosses and odd/even tasks were modeled as baseline. All statistical tests were run using custom R scripts.

Pattern Similarity Analyses

For each subject and each ROI, vectors of PEs for the grid phases for all voxels within the ROI were constructed from the model PEs using fslmeants (FSL 5.0.10). Pairwise similarities between the base grid and all five grid PEs across all four runs were calculated using Spearman's rank correlation to account for outliers due to noise in the data. Pattern similarity scores were not calculated within run to avoid confounds such as local autocorrelations. All similarity scores were then Fisher *z*-transformed. The base grid's similarity to itself across runs was not included in any of the pattern similarity analyses. For consistency with the univariate analyses, we conducted a 2x2 (object overlap x location overlap) repeated measures ANOVA with the experimental grids' similarity to the base grid as the dependent variable. Additionally, we conducted pairwise *t*-tests comparing the object overlap grid's similarity with the base grid to the

location overlap grid's similarity with the base grid, mirroring the primary univariate contrast. Pattern similarity analyses and all statistical tests were run using custom R scripts.

Pattern Similarity's Link to Behavior

Finally, we tested whether neural pattern similarity predicted behavioral performance. Specifically, we tested if markers of neural memory integration were correlated with facilitation and if markers of neural pattern separation were correlated with interference. As predictors, we calculated location similarity scores and object similarity scores from the pattern similarity analysis. We calculated the location similarity score by taking the pattern similarity of the location overlap grid to the base grid for each subject and baseline correcting it to account for individual differences. Similarly, the object similarity score was calculated by taking the pattern similarity of the object overlap grid to the base grid for each subject and baseline correcting it. For outcome variables, we created a facilitation score and an interference score. Since we used a fully crossed factorial design, we calculated these scores such that they considered all conditions. For the facilitation score, we subtracted the mean performance of the no overlap and object overlap conditions from the mean of the location overlap and full overlap conditions, such that a higher score represented improved performance when the location set was the same. For the interference score, we subtracted the mean performance of the object overlap and full overlap conditions from the mean of the location overlap and no overlap conditions, such that a higher score represented decreased performance, or greater interference, when the object set was the same. Given our small sample size (n = 21), we do not have adequate statistical power to detect individual differences. Therefore, all correlational analyses should be considered exploratory.

Results

Behavioral Performance

Since participants were pre-trained on their base grid, we expected performance on memory probe trials for their base grid to be near ceiling. Indeed, that is what we found (M = .88, SD = .06). Thus, we used the raw proportion of correct responses on the memory probe trials for the experimental grids as the primary behavioral measure. Based on our prior work (Chaloupka & Zeithamova, 2024), we hypothesized that object overlap would cause interference, leading to worse performance, and that location overlap would cause facilitation, leading to better performance. To test this, we ran a 2x2 (object overlap x location overlap) repeated measures ANOVA with the proportion of correct responses as the dependent variable (Figure 4.4). Consistent with our hypothesis, we found a main effect of object overlap, $F(1, 20) = 11.14$, p = .001, η^2_p = .41, driven by worse performance when objects overlapped (M = .63, SD = .15) compared to when objects did not overlap (M = .73, SD = .09). However, we did not find a main effect of location overlap, $F(1, 20) = 1.25$, p = .278, η^2_p = .06, as participants performed about

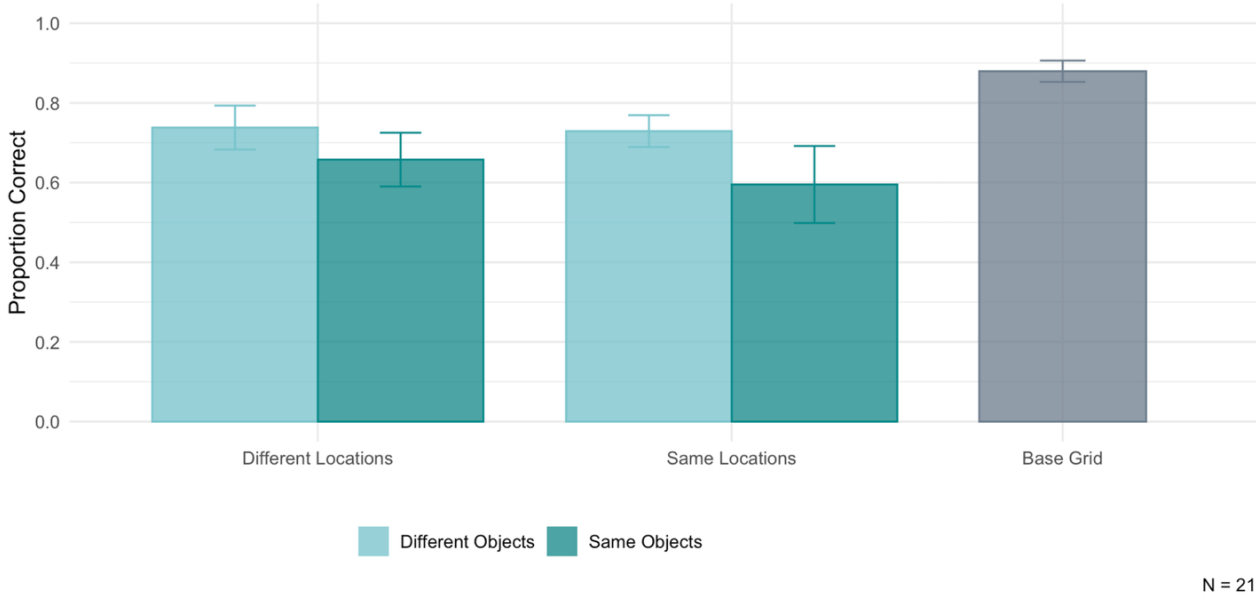

Figure 4.4. Behavioral results for the scanned sample. There was a main effect of object overlap (p = .001), but no effect of location overlap (p = .278) or interaction (p = .361). Error bars represent 95% confidence intervals.

equally well regardless of whether locations overlapped (M = .66, SD = .13) or not (M = .70, SD = .13). As expected, we found no interaction, $F(1, 20) = 0.76$, $p = .361$, $\eta^2_p = .04$.

While we failed to replicate the facilitatory effect of location overlap in this sample, we did not collect a full sample and are thus hesitant to overinterpret these results. Additionally, we did replicate our past findings in two separate pilot samples. In a pilot fMRI sample (n = 21, Figure 4.5), we used an identical response procedure, as well as the 2x2x2 (object overlap x location overlap x grid shape) design as in Experiment 2 of Chapter II. We found a main effect of object overlap, $F(1, 20) = 24.79$, $p < .001$, $\eta^2_p = .55$, driven by worse performance when objects overlapped (M = .57, SD = .19) compared to when objects did not overlap (M = .69, SD = .20). We also found a main effect of location overlap, $F(1, 20) = 9.23$, $p = .006$, $\eta^2_p = .32$, driven by better performance when locations overlapped (M = .67, SD = .18) compared to when locations did not overlap (M = .59, SD = .21). We found no interaction, $F(1, 20) = 0.11$, $p = .745$, $\eta^2_p = .01$.

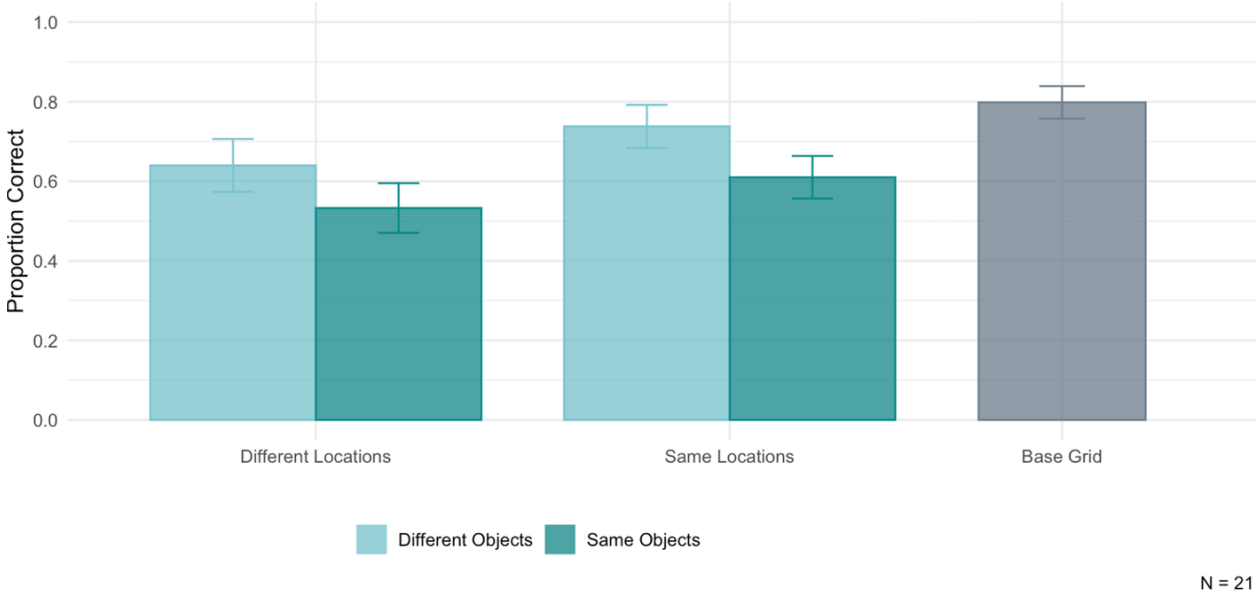

Figure 4.5. Behavioral results for the pilot fMRI sample. Results are collapsed across grid shapes. There was a main effect of object overlap ($p < .001$), a main effect of location overlap ($p = .006$), and no interaction ($p = .745$). Error bars represent 95% confidence intervals.

In a pilot behavioral sample (n = 43, Figure 4.6), we used an identical response procedure with the 2x2 (object overlap x location overlap) design. We again found a main effect of object overlap, $F(1, 42) = 23.93$, $p < .001$, $\eta^2_p = .36$, driven by worse performance when objects overlapped ($M = .69$, $SD = .19$) compared to when objects did not overlap ($M = .79$, $SD = .15$). We also found a main effect of location overlap, $F(1, 42) = 7.02$, $p = .011$, $\eta^2_p = .14$, driven by better performance when locations overlapped ($M = .77$, $SD = .15$) compared to when locations did not overlap ($M = .71$, $SD = .19$). We found no interaction, $F(1, 42) = 0.74$, $p = .395$, $\eta^2_p = .02$. In both pilot samples, object overlap caused interference and worse performance on the memory probe trials, and location overlap led to better performance. Given the consistency of the pattern of results seen across several samples and versions of the grid task, we went ahead and analyzed the neural data in this sample as planned. However, the lack of a behavioral benefit of location overlap may limit interpretability of some of the findings, especially any null results.

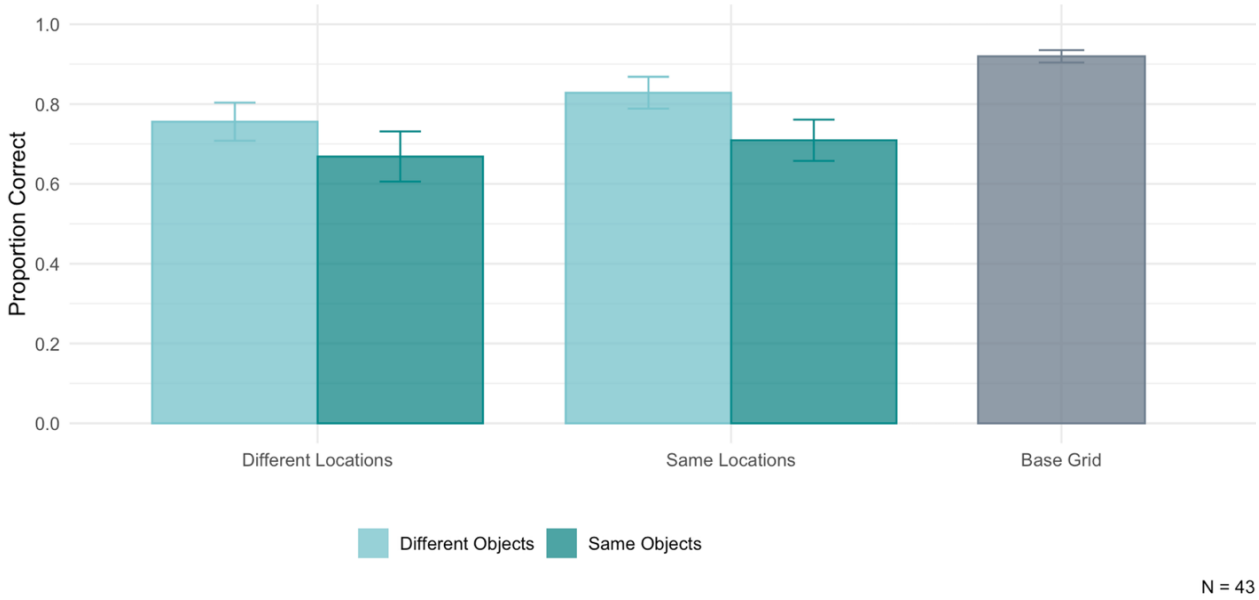

Figure 4.6. Behavioral results for the pilot behavioral sample. There was a main effect of object overlap ($p < .001$), a main effect of location overlap ($p = .011$), and no interaction ($p = .395$). Error bars represent 95% confidence intervals.

Univariate Analyses

First, we analyzed the set of hippocampal subfield ROIs. We conducted a 2x2 (object overlap x location overlap) repeated measures ANOVA with the PEs as the dependent variable (Figure 4.7A). In subiculum, we found a main effect of location overlap, $F(1, 20) = 6.03$, $p = .023$, driven by greater activation when locations overlapped compared to when locations did not overlap, although this did not survive correction for multiple comparisons. We found no effect of object overlap, $F(1, 20) = 0.09$, $p = .766$, and no interaction, $F(1, 20) = 0.16$, $p = .694$. We found no other significant effects in any of the remaining hippocampal subfield ROIs (all p's > .22).

Next, we analyzed our primary contrast of interest: object overlap vs. location overlap (Figure 4.7A). We analyzed each of the five hippocampal subfield ROIs separately. This contrast was not significant in any of the hippocampal subfield ROIs (all p's > .31).

We then analyzed the set of cortical ROIs and the whole hippocampus. Again, we conducted a 2x2 (object overlap x location overlap) repeated measures ANOVA with the PEs as the dependent variable (Figure 4.7B). We found no significant effects in any ROI (all p's > .10).

Next, we analyzed our primary contrast of interest in the set of cortical ROIs and the whole hippocampus (Figure 4.7B). We analyzed each of the five ROIs separately. We found increased activation in PHC for the location overlap condition relative to the object overlap condition, $t(20) = -2.26$, $p = .035$, although this did not survive correction for multiple comparisons. This is in line with our hypothesis that the PHC is more sensitive to spatial information. This contrast was not significant in any of the other ROIs (all p's > .31).

As a sanity check, we also analyzed a task vs. baseline contrast, where the task included all grid and probe phases, while baseline included all fixation crosses and odd/even task phases. To correct for multiple comparisons, a Bonferroni correction was applied, resulting in an alpha

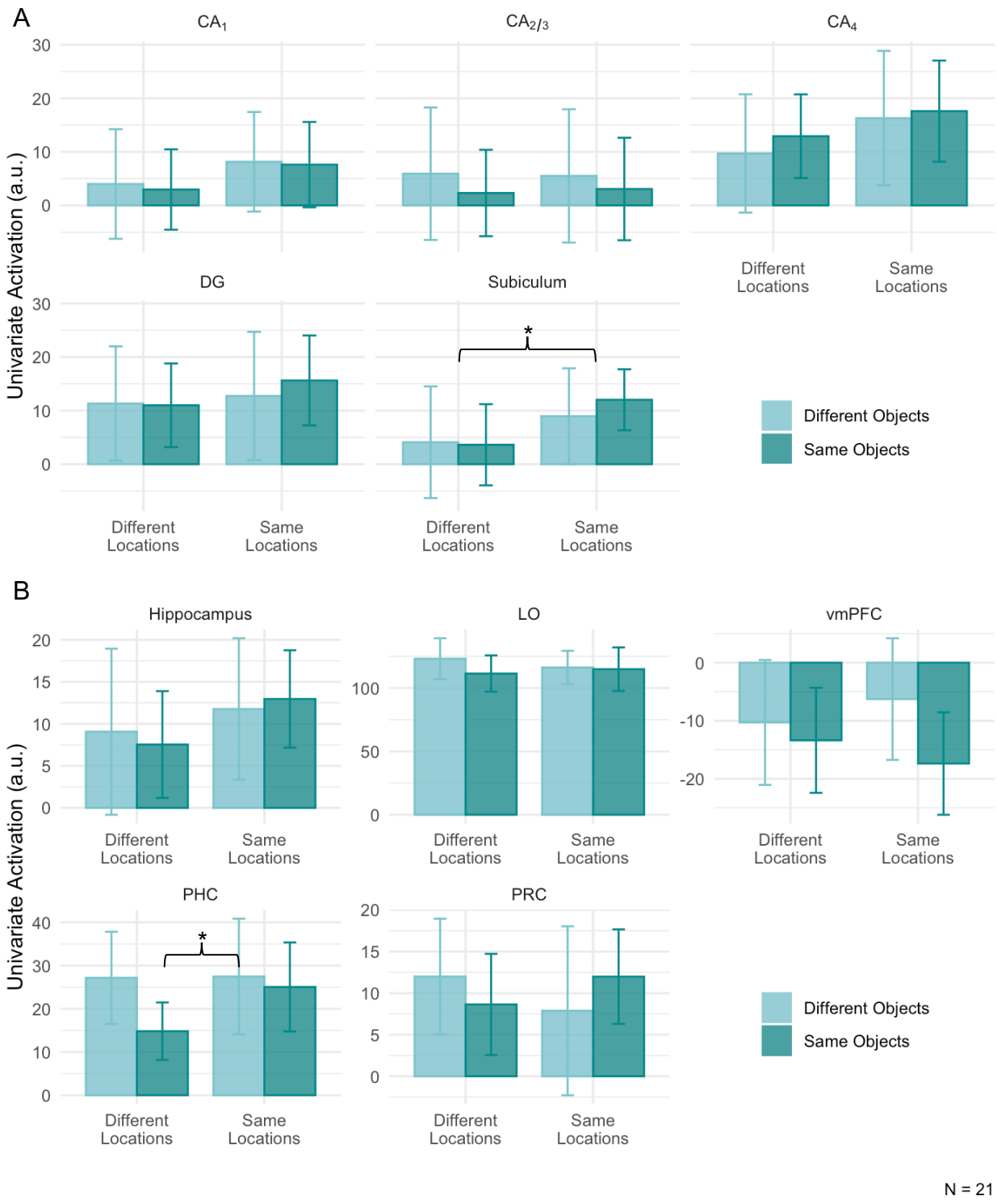

Figure 4.7. Univariate analyses. (A) Hippocampal subfields. In subiculum, there was a main effect of location overlap (p = .023). No other effects were significant in any other subfield ROI. (B) Cortical ROIs. PHC was significantly more active during the location overlap condition compared to the object overlap condition (p = .035). No other effects were significant in any other cortical ROI. Error bars represent 95% confidence intervals.

level of .01 (.05 divided by five ROIs). ROIs that were more active during the task included PRC, $t(20) = 3.46$, $p = .002$, PHC, $t(20) = 5.44$, $p < .001$, and LO, $t(20) = 13.00$, $p < .001$. Given the respective roles for each of these ROIs in the visual processing stream, this is expected. The vmPFC was more active during baseline than during the task, $t(20) = -8.31$, $p < .001$. This makes sense given the vmPFC's role in the default mode network (DMN), or task-negative network. This contrast in the hippocampus was not significant, $t(20) = -0.57$, $p = .577$, which is unsurprising given its role in learning and memory and its role in the DMN.

Pattern Similarity

First, we analyzed the set of hippocampal subfield ROIs. We conducted a 2x2 (object overlap x location overlap) repeated measures ANOVA with the experimental grids' similarity to the base grid as the dependent variable (Figure 4.8A). In DG, we found a significant interaction, $F(1, 20) = 11.27$, $p = .003$, driven by higher pattern similarity for the no overlap and full overlap grids compared to the object overlap and location overlap grids, although this did not align with our hypothesis. There was no main effect of location overlap, $F(1, 20) = 0.36$, $p = .558$, and no main effect of object overlap, $F(1, 20) = 0.02$, $p = .885$. We found no other significant effects in any of the remaining hippocampal subfield ROIs (all p's > .18).

Next, we conducted pairwise *t*-tests comparing object overlap and location overlap directly in the hippocampal subfield ROIs. We analyzed each of the five hippocampal subfield ROIs separately. The object overlap condition did not differ significantly from the location overlap condition in any of the hippocampal subfield ROIs (all p's > .35).

We then analyzed the set of cortical ROIs and the whole hippocampus. Again, we conducted a 2x2 (object overlap x location overlap) repeated measures ANOVA with the experimental grids' similarity to the base grid as the dependent variable (Figure 4.8B). We found

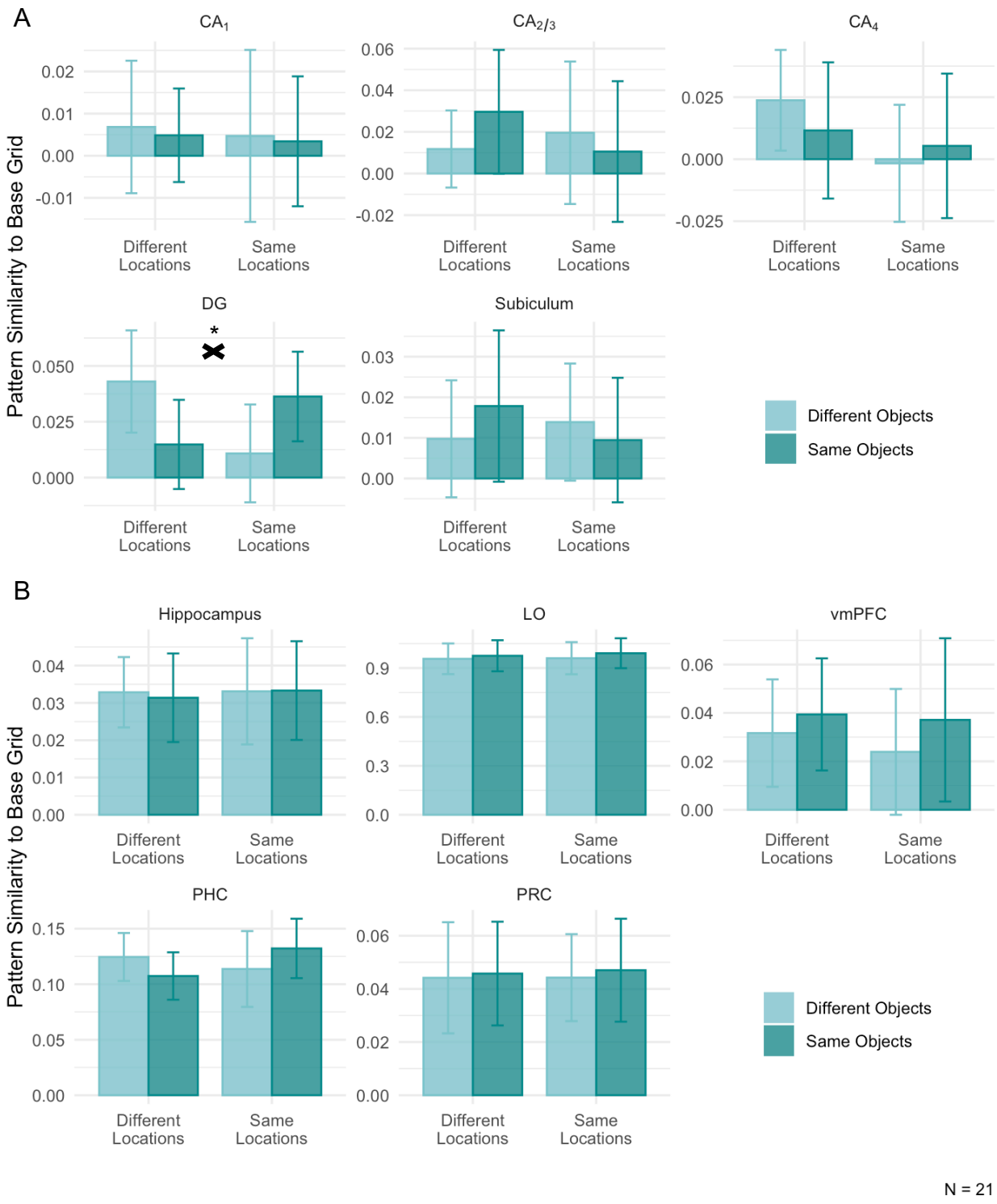

Figure 4.8. Pattern similarity analyses. (A) Hippocampal subfields. In DG, there was a significant interaction (p = .003). No other effects were significant in any other subfield ROI. (B) Cortical ROIs. There were no significant effects in any of the cortical ROIs. Error bars represent 95% confidence intervals.

no significant effects in any ROI (all *p*'s > .08). Finally, planned pairwise *t*-tests comparing object overlap and location overlap directly in the cortical ROIs and whole hippocampus did not reach significance in any of the ROIs (all *p*'s > .17).

Pattern Similarity's Link to Behavior

First, we hypothesized that neural integration in CA_1, vmPFC, and possibly PHC would lead to facilitation when locations overlapped. We tested this by correlating the location similarity scores calculated from the pattern similarity analysis with the facilitation score (performance when locations overlapped minus performance when locations did not overlap), indicative of better performance when the location set was the same between grids. In line with our hypothesis, location similarity scores in vmPFC were significantly correlated with the facilitation score, $r(19) = .56$, $p = .008$ (Figure 4.9). This indicates that an increase in baseline-

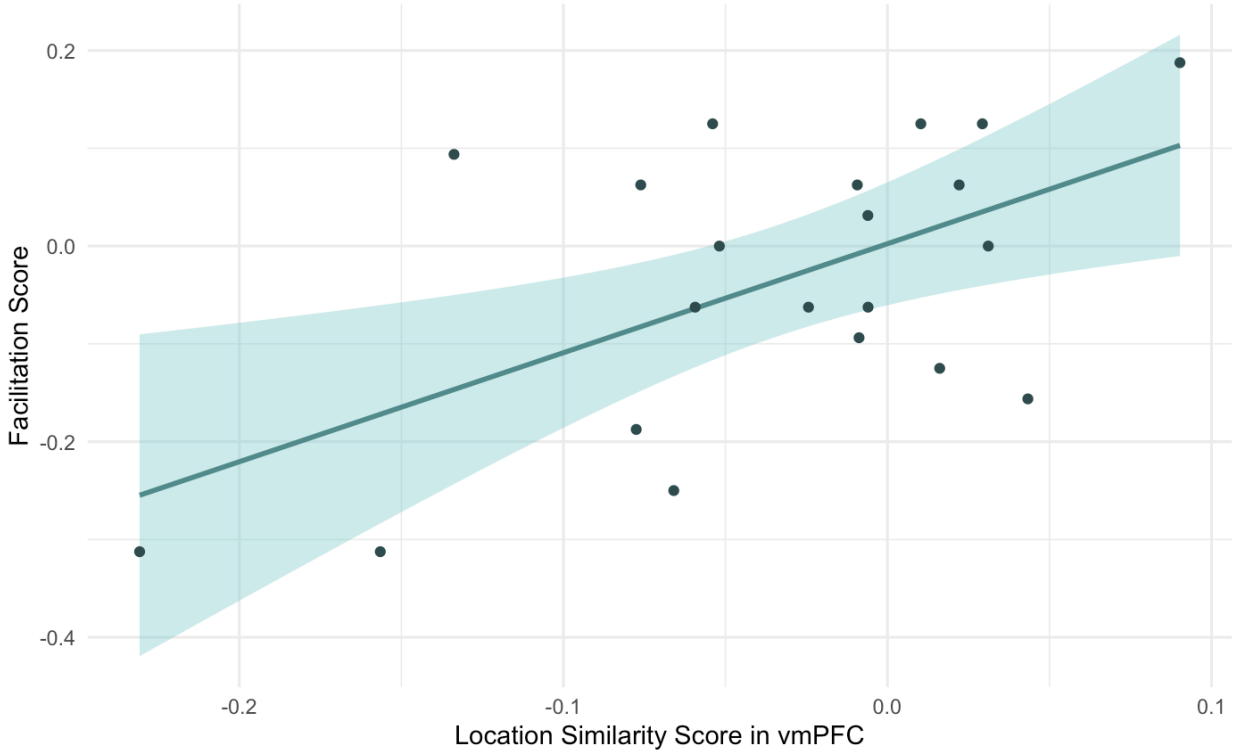

Figure 4.9. Location similarity in vmPFC and facilitation. The relationship between the location similarity score in vmPFC and facilitation score. There was a significant correlation, $r = .56$, $p = .008$. Shaded region represents 95% confidence band.

corrected pattern similarity of the location overlap grid to the base grid led to increased performance when location sets overlapped. Neither PHC, $r(19) = .04$, $p = .876$, nor CA_1, $r(19) = -.42$, $p = .06$, were significantly correlated with facilitation.

Next, we hypothesized that pattern separation or differentiation in $CA_{2/3}$ and DG would help mitigate interference driven by object overlap. We also tested the association between neural pattern similarity and behavioral sensitivity to object overlap in PRC, as an object-selective region. We tested these hypotheses by correlating the object similarity scores calculated from the pattern similarity analysis with the interference score (performance when objects did not overlap minus performance when objects overlapped), indicative of worse performance, or greater interference, when the object set was the same between grids. This was not significant in any of the ROIs (all p's > .15).

Discussion

Here, we used a novel grid task to examine how the brain supports facilitation and mitigates interference under two distinct types of overlap. Univariate analyses revealed that the subiculum was more active when locations overlapped and that PHC was more active during the location overlap condition compared to the object overlap condition. Using pattern similarity analyses, we found a significant interaction in DG, but no other significant effects. However, location similarity scores in vmPFC were related to facilitation.

In line with our hypothesis, we found that the PHC was more active during the location overlap condition when compared to the object overlap condition. This confirms the PHC's role in processing spatial information. We did not find evidence that the vmPFC was more active during the location overlap condition, although numerically the effect was in the expected

direction. It is possible that this did not reach significance due to either the small sample size or lack of a behavioral effect, although additional studies are needed to reach a final verdict.

While pattern similarity analysis revealed no effects in vmPFC, we did find that the location similarity score in vmPFC was positively related to behavioral facilitation, consistent with our hypothesis. This may suggest that some participants were forming a spatial schema, and that doing so provided greater facilitation when locations overlapped. While this would typically be considered quite fast for schema formation, Tompary and colleagues (2020) found that schemas may actually form quite quickly. While this finding is promising, other mechanisms may be responsible for our findings, and our small sample size renders this analysis exploratory, so future work is necessary to elucidate this relationship.

We found no evidence that univariate activity in PRC was driven by overlapping objects. Additionally, pattern similarity analyses revealed no effect of object overlap in PRC. While it is well known that the PRC tracks object identity (Miyashita, 2019; Tamura et al., 2017), this evidence largely comes from experimental designs in which participants view only one object at a time. Thus, our lack of findings may be due to the grid stimuli used in which there is an entire set of objects rather than a single object.

Surprisingly, we found no evidence for pattern separation in $CA_{2/3}$ or DG. Additionally, the level of pattern separation was not linked to behavioral interference in either subfield. It is not entirely surprising that we failed to find a link to behavior, given the exploratory nature of this analysis with such a small sample size. However, the lack of pattern separation fails to support our hypothesis as well as the prior literature (Bakker et al., 2008; Chanales et al., 2017; Favila et al., 2016; Leutgeb et al., 2007; Yassa & Stark, 2011). It is possible that the design of

the task was not optimized for pattern similarity analyses, as we found no significant effects of interest.

Contrary to our hypothesis, we found no evidence for the involvement of CA_1 in facilitation via memory integration. While there is some evidence for the role of CA_1 in integration (Schlichting et al., 2014; Schlichting & Preston, 2015), the precise nature of this role remains an open question. Despite failing to find anything of interest, this should not necessary be interpreted as a lack of involvement of CA_1 in schema-related learning but rather may indicate the limitation of the grid task used in this study. While we interpreted the facilitation effect as the result of an early spatial schema, it is more typical for schemas to facilitate new learning after they have been firmly entrenched over the course of at least several days. Additionally, we failed to find a behavioral effect of facilitation, rendering the possibility that this sample of participants simply failed to integrate grids that shared locations.

Limitations and Future Directions

The most glaring limitation of this study is the small sample size (n = 21). Data collection continued until we ran out of funding for this project. Based on a power analysis for the behavioral ANOVA, our target sample size was 40. To sufficiently power statistical tests for the links from neural measures to behavioral outcomes, we would have needed an even larger sample size. Thus, while some of our findings are promising, confirmatory experiments are needed to confirm these results with adequately powered samples.

A second limitation to this study is the within-subjects design. The design used for this study had participants overlearn a base grid, which they returned to as a way to reset between each experimental condition. This design may lead to a steady buildup of interference, above and beyond the interference caused by overlapping objects. By the end of a single run, participants

have seen five different grids and switched between grids seven times. Since this data was collected, we have designed a new within-subjects version of the task. In the new design, we drop the full overlap condition since the behavioral effects of location overlap and object overlap never interact. This reduces the design to a one-way ANOVA with three levels. Additionally, we use the preceding grid as the comparison for each subsequent grid, rather than a static base grid. For example, the second grid may overlap with the first in objects, the third grid overlaps with the second in locations, and the fourth grid doesn't overlap with the third at all. This design requires that participants only see four total grids and switch between grids only three times, reducing the overall buildup of interference throughout the task.

Another design limitation concerns the response procedure used in this task. Ideally, an MRI-compatible joystick or similar device could be used so that participants could recreated the entire grid. Since we are interested in how well participants learn the grid as a whole, this provides a better operationalization of successful learning than memory for individually probed items. If memory probes must be used, a balanced design may improve upon the design used here, such as the one described in Chapter III. Future work is needed to determine the best task design to measure learning of the full set of object-location associations.

Conclusions

In summary, we found that medial temporal regions differentially represented overlapping events, and that pattern integration in vmPFC promoted facilitation. Specifically, PHC was preferentially active during the location overlap condition. We also found that the level of the location similarity score in vmPFC was positively related to behavioral performance when grids shared a set of locations. Our findings shed some new light on how the brain supports

facilitation and mitigates interference in an object-location association task and lays the foundation for concurrent investigation of these two related phenomena.

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CHAPTER V

GENERAL DISCUSSION

In this dissertation, we focused on the central question of why overlapping experiences facilitate new learning in some cases but interfere with learning in others. In Chapter I, we reviewed the literature on facilitation and interference, two disparate outcomes of overlapping experiences. In Chapter II, we introduced a novel behavioral paradigm – an object-location paired-associates grid task – designed to disentangle these differential effects. We found that overlapping locations facilitated new learning while overlapping objects caused interference. In Chapter III, we explored an alternate version of the grid task, providing partial evidence that both effects generalize across different versions of the task. In Chapter IV, we examined the neural mechanisms underlying both facilitation and mitigation of interference. We found that the level of pattern integration in the ventromedial prefrontal cortex (vmPFC) was positively related to behavioral performance. We also found that the parahippocampal cortex (PHC) was preferentially active during the location overlap condition. Collectively, our findings demonstrate that different types of overlap differentially affect new learning and provide some insight into the brain processes underlying these effects.

Facilitation and Schemas

As summarized in Chapter I, there is an extant body of literature on facilitation via schemas (Attneave, 1957; Bartlett, 1932; King et al., 2019; Posner et al., 1967; van Kesteren et al., 2014). Schemas – complex mental representations – facilitate learning when new information overlaps with previously learned information. Furthermore, the more similar new information is to old information, the more quickly it is learned. If we return to our first scenario from above, we can see that this is the case. Your schema of campus facilitates your ability to learn the

locations of your classes and meetings each term. Additionally, the more similar the locations, the quicker they are to learn. For example, if you have a class in an adjacent room in the same building as the term before, this location will be easier to learn than that of a class in a new building across campus. In this example, the information that overlaps between terms is the spatial framework of locations across campus.

Evidence suggests that spatial schemas are especially effective at facilitating new learning. A seminal paper by Tse and colleagues (2007) demonstrated this effect using a flavor place paired-associates task with rats. After learning a spatial schema, the rats were able to quickly learn new information. The facilitatory effect of spatial schemas has since been confirmed in humans (Guo & Yang, 2020; Kyle et al., 2015; van Buuren et al., 2014). The behavioral evidence presented in Chapters II-IV is in line with existing literature. In five out of seven experiments, we found that overlapping locations in an object-location association grid task facilitated learning and memory. Given that participants completed the grid task in a single session, we cannot conclusively say that the source of this facilitation was a spatial schema. However, some evidence suggests that schemas may form quickly, even if they aren't relied on until episodic memories begin to fade (Tompary et al., 2020).

Our findings add to the ever-growing catalog that suggests that spatial information holds a unique role in memory organization. For example, one study found that location familiarity increases the vividness of imagined future events (Arnold et al., 2011). Another study found that location context cues were more effective at recall than person context cues, and participants spontaneously generated location cues if they were given person cues, but not vice versa. Additionally, spatial information is the core of the method of loci memory strategy, which has been shown to be a highly effective mnemonic device (Ross & Lawrence, 1968; Wang &

Thomas, 2000). Here, we have demonstrated that location overlap facilitates learning and memory in an object-location association task, while object overlap does not. Therefore, our results strengthen the theory that spatial information plays a special role in learning and memory.

Memory Interference

Chapter I also provides a summary of the extensive body of literature on memory interference. Specifically, overlapping experiences hinder new learning via proactive interference – when memory of old information is detrimental to learning of new information (Bergstrom, 1893; Bunting, 2006; Dallet & Wilcox, 1968; Goggin & Wickens, 1971; Keppel & Underwood, 1962; Maslow, 1934; Melton & von Lackum, 1941; Underwood, 1957; Wickens et al., 1963; Wixted & Rohrer, 1993). Our second example above illustrates this well. While the students in your class remain the same, your knowledge of the prior seating arrangement interferes with your ability to locate your students in their new seats.

While the interference literature suggests that overlap hinders learning and memory, the type of information that overlaps is somewhat consistent across these studies. Often, they are written in the form of 3-consonant syllables (Keppel & Underwood, 1962; Melton & von Lackum, 1941; Wickens et al., 1963), words (Bunting, 2006; Dallet & Wilcox, 1968; Goggin & Wickens, 1971; Wixted & Rohrer, 1993), number strings (Bunting, 2006; Wickens et al., 1963), or in the case of our example, names of students. The findings presented in Chapters II-IV are consistent with previous research. In six out of seven experiments, we found that overlapping objects in an object-location association grid task interfered with new learning. Collectively, this evidence suggests that interference occurs when the content of experiences overlaps.

The Dual Effect on Associative Learning

Prior work indicates that proactive interference also affects associative learning (Kliegl & Bäuml, 2021; Postman et al., 1974; Tulving & Watkins, 1974). Associative learning is often studied using the classic AB/AC task, in which participants first learn one set of paired-associates (AB) followed by a second set of overlapping (AC) or non-overlapping (DE) paired-associates. Historically, studies have demonstrated that AC associations are harder to learn than DE associations due to the interference caused by their overlap with the previously learned AB associations. However, the stimuli used in these tasks are typically objects or words, stimulus types that individually have been shown to elicit interference when similar or overlapping. The grid task presented in this dissertation uses an associative learning paradigm, but one in which one side of each paired-associate is an object while the other half is a location. While the task used by Tse and colleagues (2007) used a flavor-location paired-associates task, flavors were changed entirely for new pairs, and new locations were always adjacent to a previously learned location. The paired-associates tasks used by van Buuren and colleagues (2014) and Guo and Yang (2020) also used object-location associations, but only manipulated the pairings within a fixed object set and fixed location set. Thus, no study had investigated how manipulating both the object and location set affects new learning.

The grid task introduced in Chapter II offers a novel paradigm that uses object-location paired-associates. Critically, both the object and location set are manipulated in the task. Participants learn a set of object-location pairs on a grid to criterion and then are randomly assigned to learn a second grid that overlaps in objects, locations, both, or neither. When the second grid overlaps in objects, participants are slower to learn, consistent with interference theory. When the second grid overlaps in locations, participants are faster to learn, consistent

with facilitation theory. This task was the first to use object-location pairs and manipulate which piece of the pair overlapped, allowing us to observe that the type of overlap – objects or locations – determines the direction of the effect on new learning.

Replication Across Multiple Variations of the Task Design

The two experiments reported in Chapter II offer consistent and robust findings, demonstrating that location overlap facilitates new learning and object overlap interferes with new learning. The task design used in these experiments requires that participants recreate the entire grid of object-location associations by dragging and dropping objects to their locations on the grid and measures the number of trials to criterion as an operationalization of learning rate. For the purposes of creating an MRI-friendly version of the task and to ensure that the facilitatory effect of location overlap is not an artifact of the drag-and-drop procedure, we designed alternate versions of the task with different types of memory probes as the response procedure. In Chapter III, we introduce a between-subjects design in which two balanced types of memory probes are used in the response phase. One type requires the participant to choose the location of a single object, while the other requires them to choose the object that belongs to a single location. In Chapter IV, we introduce a within-subjects design that utilizes a single type of memory probe. Here, participants must select the correct location for a single object, but the location foils are chosen such that one belongs to the studied location set, one from the alternate location set, and one from neither set, as opposed to all of the options belonging to the studied set. While we did run into various problems along the way, we found a facilitatory effect of location overlap in three of the five experiments reported in Chapters III and IV, and an interference effect of object overlap in four of the five experiments. This suggest that these effects generalize to a memory probe response procedure and can be observed within-subject.

Neural Effects of Location Overlap

Prior work has identified the PHC as a brain region that is sensitive to spatial information (Epstein & Baker, 2019; Epstein & Kanwisher, 1998; Sun et al., 2021). In particular, Epstein and Kanwisher (1998) labeled a specific region within the PHC as the 'parahippocampal place area' – a region that selectively responds to location or scene information. As hypothesized in Chapter IV, we found increased activation in PHC in the grid task when locations overlapped compared to when objects overlapped. This conforms to the literature, demonstrating that the PHC is sensitive to spatial information in the grid task.

The vmPFC has been implicated in schema formation (Gilboa & Marlatte, 2017; Robin & Moscovitch, 2017; van Kesteren et al., 2012). In Chapter II, we suggest that the behavioral effect of facilitation as an outcome of location overlap may be due to the early formation of a spatial schema. In Chapter IV, we found that participants with a higher level of pattern integration for the location overlap grid in the vmPFC demonstrated greater facilitation in the grid task. This finding provides some evidence for the early formation of a spatial schema in participants. While it was long assumed that schemas take a long time to form, recent evidence suggests that schemas may actually form quickly, but we rely on our episodic memories until those begin to fade (Tompary et al., 2020). Thus, some participants may have begun to form a spatial schema quite quickly, and thus better leveraged the facilitation effect of overlapping locations. To further test this idea, increased and varied delay times could be incorporated into the grid task to determine the timeline of the formation of a spatial schema.

Neural Effects of Object Overlap

Research has shown that the PRC is involved in object recognition (Bartko et al., 2007b, 2007a; Miyashita, 2019; Tamura et al., 2017). This has been investigated using individual object

stimuli, so the involvement of the PRC in the grid task, which uses sets of eight objects, was an open question. In Chapter IV, we failed to find evidence that the PRC was sensitive to object overlap using univariate and pattern similarity analyses. This suggests that the PRC may be specialized in tracking the identity of individual objects rather that a set of objects. However, further research is needed to verify this given the limitations of the study reported in Chapter IV.

The hippocampal subfields CA_3 and dentate gyrus (DG) have been shown to mitigate memory interference via pattern separation – when activation patterns for similar stimuli become uncorrelated (Bakker et al., 2008; Leutgeb et al., 2007; Yassa & Stark, 2011), or even differentiation or repulsion – when activation patterns for similar stimuli become negatively correlated (Chanales et al., 2017; Favila et al., 2016). Greater pattern separation leads to more distinct representations of similar stimuli in CA_3 and DG, thereby reducing interference and increasing memory performance. In Chapter IV, we failed to find evidence for pattern separation in either subfield. However, the grid task design used in this study may not have been optimized for pattern similarity analysis, so we hesitate to overinterpret these null effects.

Limitations and Future Directions

While the findings presented in Chapters II-IV provide compelling results that elucidate some of the nuances of how overlapping experiences shape learning and memory, there are some limitations to the experiments reported in this dissertation. One challenge we encountered was how to best probe participants' memory for the object-location associations and track their learning. While the original design used in Chapter II is simple and effective, it has some minor flaws. The drag-and-drop procedure may emphasize the importance of the location information in the task. Additionally, participants must choose from all possible locations on the grid, while only the eight objects from the studied set are presented, creating an imbalance between the two

sides of the paired-associates. It is not fully understood whether this is problematic, as participants must learn the full grid of object-location associations for the task to measure the variable in question. Nonetheless, we aimed to assuage any concerns in Chapter III by introducing a new response procedure with two types of memory probes. While we managed to replicate the results from Chapter II in our first experiment, an error in the condition files prevents this from being indisputable. In a second experiment, we observed a ceiling effect, highlighting additional challenges with the memory probe response procedure. For example, the dependent variable of interest is the rate of new learning, but probing a single object from the grid at a time is a less precise way of capturing this than requiring participants to retrieve the entire set of object-location associations. Many attempts to eliminate the ceiling effect in the memory probe design, such as decreasing exposure time or increasing the number of associations in the set, would further reduce the ability of a single-object memory probe to truly measure learning rate of the entire grid. Thus, while the original design used in Chapter II may be closer, future work is needed to develop the ideal response procedure for the grid task.

The grid task is optimal for a between-subjects design, because increasing the number of grids a participant studies causes a steady buildup of interference over the course of the experiment, muddling the effects of the manipulated variables. However, a between-subjects design increases the number of participants needed, is less effective at accounting for individual differences, and is suboptimal for fMRI data collection. In Chapter IV we implemented a within-subjects design for the scanned sample, in which participants were trained on a 'base grid' and returned to this grid between each experimental grid. Participants studied a total of five different grids in this design and were exposed to their base grid far more often than any of the other grids. In an ongoing study, we have implemented a new within-subjects approach in which each

condition is determined by comparing performance on a given grid to its preceding grid. Since we reliably find no interaction between object overlap and location overlap, we ran this version without the full overlap condition. Thus, participants only study four grids and learn each grid in a single block. This design has yielded encouraging results, finding that location overlap facilitates learning of a subsequent grid, while object overlap interferes with learning of a subsequent grid.

In Chapter IV, we presented some interesting neural findings. However, the primary limitation of this experiment is the small sample size (N = 21). This is roughly half of the desired sample size, and therefore all analyses of this sample are underpowered. Follow-up studies are needed to confirm our findings. Another limitation of the scanned task is the constraints on participant responses in the MRI scanner. Use of button boxes necessitated that we use a memory probe response procedure similar to the one used in Chapter III. However, future studies could utilize an MRI-compatible joystick so that participants could reconstruct the entire grid while in the scanner.

Conclusion

In summary, we found across several experiments that different types of overlap differentially affect new learning. In a novel object-location association grid task, we found that overlapping objects interfered with new learning while overlapping locations facilitated new learning. These effects mostly generalized to an alternate response procedure, demonstrating that the facilitatory effect of location overlap is not limited to a drag-and-drop procedure that puts emphasis on the spatial information, and providing a feasible design for fMRI data collection. We confirmed that the PHC was more sensitive to location overlap and that location similarity in the vmPFC was positively correlated with behavioral performance. This may indicate that some

participants were forming a spatial schema. Collectively, our findings help elucidate the idiosyncrasies of distinct types of overlap, provide insight into how the brain differentially supports facilitation and mitigates interference depending on the type of overlap, and sets the stage for a unified investigation of facilitation and interference.

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