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https://doi.org/10.7275/10006390 https://scholarworks.umass.edu/masters_theses_2/544

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A REPRESENTATIONAL-HIERARCHICAL ACCOUNT: A NEW THEORY OF FALSE MEMORIES

A Thesis Presented

by

D. MERIKA WILSON

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

May 2017

Psychological and Brain Sciences

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A REPRESENTATIONAL-HIERARCHICAL ACCOUNT:
A NEW THEORY OF FALSE MEMORIES

A Thesis Presented

by

D. MERIKA WILSON

Approved as to style and content by:

_____
Rosemary A. Cowell, Chair

_____
Rebecca Spencer, Member

_____
Jeffrey Starns, Member

_____
Caren Rotello, Department Head
Psychological and Brain Sciences

ABSTRACT

A REPRESENTATIONAL-HIERARCHICAL ACCOUNT: A NEW THEORY OF FALSE MEMORIES

MAY 2017

D. MERIKA WILSON, B.S., ST. LAWRENCE UNIVERSITY

M.S., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Dr. Rosemary A. Cowell

Past research has supported a representational-hierarchical theory of memory and perception that extends the ventral visual stream into the medial temporal lobe. In this account, representations are organized in a hierarchical manner, such that structures located further anterior in the brain contain complex representations of whole objects and areas further posterior in the visual cortex contain representations of simple features. When conjunctive representations are compromised, an individual must rely on simple-feature representations to complete mnemonic and perceptual tasks. However, these simple-feature representations are susceptible to feature-level interference, which can cause false recognition of novel objects. The goal of the present study was to explore the account's third assumption: the effect of interference. Experiment 1 examined the effect of interference on neural representations during fMRI. Experiment 2 investigated the effect of different types of interference on a behavioral memory task with older adults thought to have impaired conjunctive representations. Although the results of the first experiment were inconclusive, the second experiment revealed that older adults' recognition memory performance was shielded from semantic, but not perceptual, interference. The implications of this finding are discussed.

TABLE OF CONTENTS

Page

ABSTRACT iv

LIST OF TABLES vii

LIST OF FIGURES viii

CHAPTER

1. THE REPRESENTATIONAL-HIERARCHICAL THEORY 1

1.1 Introduction 1

1.1.1 The Representational-Hierarchical Account of Perceptual Findings 4
1.1.2 The Representational-Hierarchical Account of Memory Findings 6

1.2 Aims 11

2. EXPERIMENT 1 13

2.1 Testing the Theory with Neural Evidence in Healthy Young Adults 13
2.2 Method 17

2.2.1 Participants 17
2.2.2 Materials 17
2.2.3 Procedures 17

2.2.3.1 Task 20
2.2.3.2 Functional Localizer 20
2.2.3.3 Image Acquisition and Preprocessing 21
2.2.3.4 Definition of Regions of Interest 22

2.2.4 Statistical Analysis 22

2.2.4.1 Repetition Reduction Analysis 22
2.2.4.2 Pattern Similarity Analysis 23

2.3 Results 26

2.3.1 Behavioral Performance 26
2.3.2 Repetition Reduction Analysis 26

2.3.3 Pattern Similarity Analysis 27

2.4 Discussion 27

3. EXPERIMENT 2 30

3.1 Testing the Theory with Behavioral Evidence in Aging Populations 30
3.2 Methods 34

3.2.1 Participants 34
3.2.2 Materials 35
3.2.3 Procedures 36

3.2.3.1 Task 37
3.2.3.2 Neuropsychological Tests 37

3.2.4 Statistical Analysis 38

3.2.4.1 Signal Detection Model 38
3.2.4.2 Univariate Analysis 42

3.3. Results 43

3.3.1 Neuropsychological Test Performance 43
3.3.2 ANOVA Results 43

3.4 Discussion 46

4. GENERAL DISCUSSION 52

4.1 Overview of Findings and Future Directions 52

APPENDICES

A. EXPERIMENT 2 SEMANTIC WORD LISTS 68
B. EXPERIMENT 2 PHONEMIC/ORTHOGRAPHIC WORD LISTS 69
C. EXPERIMENT 2 EXTRA WORDS 70

REFERENCES 71

LIST OF TABLES

Table Page

1. Older Adult Average Raw Scores for Neuropsychological Battery 54

LIST OF FIGURES

Figure Page

1. Illustration of Shared Posterior Simple Features and Unique Anterior Conjunctions of Features 55

2. Predicted Changes in Repetition Reduction (RR) and Pattern Similarity (PS) after a Long Series of Same-Category Images in High Interference Runs 56

3. Examples of a Same Category (High Interference) and an Other Category (Low Interference) Run....57

4. Effects of ROI, Section, and Interference on Repetition Reduction (RR)....58

5. Effects of ROI, Section, and Interference on Pattern Similarity (PS) 59

6. Effects of ROI and Interference on Pattern Similarity (PS) Difference between Section 1 and 4 60

7. Predicted DRM Performance for Older Adults 61

8. Illustration of Signal Detection Theory Measurements....62

9. Proportion of Times a Confidence Level was used by Older and Young Subjects....63

10. Illustration of the Process to Obtain d' Values of Interest for a Condition 64

11. Effects of List Length, List Type, Item Type, and Age Group on Discriminability from Targets....65

12. Comparison of Ly et al.'s (2013) List Type and Age Group Effects on Related Lure Discriminability from Targets....66

13. Effects of List Type, Item Type, and Age Group on Study-Related Interference for Discriminability from Targets....67

CHAPTER 1

THE REPRESENTATIONAL-HIERARCHICAL THEORY

1.1 Introduction

Early research on the organization of the brain was largely influenced by studies of patients with lesions and other brain damage that result in impaired cognitive functions. This research has been framed within a modular paradigm in which a region of the brain is specialized for a specific function (Bussey & Saksida, 2007). Most notably, studies of patient H.M. indicated that structures within the medial temporal lobe (MTL), including the hippocampus, parahippocampal, entorhinal and perirhinal cortices, are crucial for encoding, storage and retrieval of memories for events and facts (Scoville & Milner, 1957). A more thorough description of the processes involved in these areas was put forth in a theory termed the MTL memory system account (Squire & Zola-Morgan, 1991). In this system, the structures of the MTL are important for establishing long-term declarative memories, but do not have a role in perception. However, in contrast to the MTL memory system account, more recent evidence suggests that the MTL is involved in both memory and perception (Barense et al., 2005; Barense, Gaffan, & Graham, 2007; Barense, Henson, Lee, & Graham, 2010; Bartko, Winters, Cowell, Saksida, & Bussey, 2007b; Lee, Buckley, et al., 2005; Lee, Barense, & Graham, 2005).

The representational-hierarchical theory provides an account of *how* the MTL is involved in these two cognitive processes. The version of the representational-hierarchical account detailed here explains object perception and object recognition memory by exploring the types of representations contained in the ventral visual pathway

and MTL. The model assumes a hierarchical organization of object representations within the ventral visual stream, a scheme assumed by many models of object vision. In this hierarchy, areas more posterior in the brain contain representations of very simple visual features (Hubel & Wiesel, 1962, 1965) and the more anterior a structure is, the more conjunctive the visual representation contained within that area (see Figure 1) (Desimone & Ungerleider, 1989; Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001). A representation's "conjunctiveness" is determined by how many simple features are conjoined at that level of the hierarchy. For example, an apple may be processed as separate simple features of color, size, shape and texture in more posterior regions, those simple features may be combined into a simple conjunction of size and shape in intermediate regions, and a whole apple may be represented in an anterior brain area. These conjunctive representations are critical when simple features are insufficient to distinguish between different objects during familiarity and perceptual discrimination tasks.

The notion of conjunctive representations under the representational-hierarchical account was first used to explain the controversial function of a brain region within the MTL, the perirhinal cortex (PRC). Since Squire & Zola-Morgan (1991), it has been widely accepted that the PRC is involved in recognition memory. There is also evidence to support PRC's role in perception, but only under certain circumstances (see Section 1.1.1: Large stimulus set sizes and configural tasks) (Buckley & Gaffan, 1997; Lee, Buckley, et al., 2005). The representational-hierarchical account explained these perceptual findings by proposing that all of the tasks on which PRC lesions caused impairments involved feature ambiguity. Feature ambiguity is a property of a task involving visual stimuli that occurs when simple features are repeated across different

visual stimuli. The PRC was proposed to be critical for these tasks because it can resolve feature ambiguity.

Within the representational-hierarchical account, stimulus discrimination is made possible by the PRC because it contains conjunctions of visual features corresponding to a whole object, such as the conjunction of color, shape, size and texture into a representation of a whole apple. The conjunctive PRC representations are selective for the exact conjunction they represent. For example, if a neural representation is selective for an apple (the conjunction of red/orange color, round shape, size smaller than a fist, and smooth texture), it will be much more active during a perceptual discrimination task for an apple than for a peach (a conjunction of red/orange color, round shape, size smaller than a fist, *but* fuzzy texture). The PRC represents the stimuli as two unique objects and not as two highly overlapping collections of simple features because the objects differ in at least one feature (texture) (Bussey & Saksida, 2002). In contrast, perceptual discrimination between the highly similar apple and peach based on feature-level representations is considerably more difficult because the representation of the apple will only be 25% more active for apple than for peach. Thus, the whole conjunctive representation stored in the PRC provides more information that uniquely identifies an object than the sum of its simple-feature representations in posterior areas.

If the PRC is lesioned, the conjunctive representations are compromised and tasks involving visual stimuli must be solved on the basis of simple visual feature representations housed in more posterior brain areas. According to the representational-hierarchical account, the reliance on simple-feature representations causes impairments in perception and memory, most notably demonstrated in poor performance in oddity tasks

(Bartko et al., 2007b; Buckley, Booth, Rolls, & Gaffan, 2001; Lee, Buckley, et al., 2005) and false recognition of novel items (McTighe, Cowell, Winters, Bussey, & Saksida, 2010). Empirical findings demonstrating these mnemonic and perceptual impairments and their relation to the model are discussed in further detail in the two following sections.

1.1.1 The Representational-Hierarchical Account of Perceptual Findings

The representational-hierarchical theory accounts for the effects of PRC lesions reported in the existing object perception literature. First, it was demonstrated that the PRC is needed for visual object discrimination tasks. Monkeys were trained to discriminate between simultaneously presented pairs of visual stimuli (all pairs were repeatedly presented, with only one stimulus in each pair being associated with reward) (Buckley & Gaffan, 1997). After training, the monkeys had the PRC surgically removed and performed the visual discrimination task again. The now PRC-lesioned monkeys performed poorly on the discrimination task with the preoperatively learned stimuli. However, the monkeys successfully discriminated between new postoperatively learned stimuli unless the task involved a greater number of distractors. The PRC appeared to be involved in visual discrimination only under specific conditions.

The representational-hierarchical theory can explain both preoperative retention and postoperative learning effects. Impaired retention of preoperatively learned discriminations occurs because the PRC conjunctive representation of those stimuli, which were associated with reward during preoperative learning and enabled performance of the task, no longer exists (Bussey & Saksida, 2002). Further, visual

discrimination of postoperatively learned stimuli may be possible based on posterior simple-feature representations alone; however, impairments develop with increasing set size. As the set size increases, the probability that simple features are shared by more than one object, and, critically, by both rewarded and non-rewarded objects, is greater, and thus feature ambiguity increases. When PRC conjunctive representations are absent, this feature ambiguity cannot be resolved using the simple-feature representations that remain in posterior visual cortex and discrimination between two similar objects fails.

The above representational-hierarchical theory explanation is supported empirically by the finding that PRC-lesioned patients can distinguish objects based on obvious simple features; yet, they demonstrate deficits in any discrimination task that requires the use of complex, conjunctive representations (Lee, Buckley, et al., 2005). For example, PRC-lesioned subjects are able to discriminate between two objects that differ in terms of color or size, but show impairments in matching whole objects across different viewpoints. Discrimination using simple features is intact because these patients' simple-feature representations in posterior visual cortex are preserved. However, discriminations involving different viewpoints require conjunctive representations because simple features must be combined to accurately create three-dimensional viewpoint independent representations. These early empirical results, together with the explanation offered by the representational-hierarchical account, suggested two novel conclusions: (1) structures within the MTL, as well as structures in the ventral visual stream, play an important role in perception, and (2) the involvement of a given brain region in a particular perceptual task depends upon whether the task requires the types of stimulus representations housed in that region.

As demonstrated by these findings, the representational-hierarchical theory provides an account of perception that extends the hierarchy of stimulus representations in the ventral visual stream into the MTL. In healthy participants, objects with overlapping features do not cause discrimination deficits because the PRC, which represents complex conjunctions of features, distinguishes between items based on the whole object representation. However, in individuals with MTL damage, who lack the conjunctive representations in PRC that uniquely identify a complex object, the brain is forced to rely upon simple-feature representations in earlier visual cortical regions. In this case, the feature ambiguity cannot be resolved and discriminability deficits ensue. Importantly, this account does not claim that the PRC is strictly a perception region. Rather, the representational-hierarchical theory is an account in which brain regions are specialized for housing representations at a specific level of complexity, not for performing specific functions; thus, each brain region can contribute to any cognitive function, including memory, perception or even other cognitive functions such as categorization.

1.1.2 The Representational-Hierarchical Account of Memory Findings

In addition to accounting for the role of MTL structures in perception, the representational-hierarchical account also provides a mechanistic account of the effects of PRC damage on memory, as measured with the object recognition memory paradigm. Object recognition memory tasks are frequently used to test declarative memory because responses can be recorded from both animals and humans without requiring aspects of cognition that are unique to humans, such as spoken language. Further, a finding of a

delay-dependent deficit following PRC lesions is critical to the demonstration that PRC is involved in *memory*, because an increase in delay between the time of study and the time of test is assumed to provide a manipulation of memory load.

Eacott, Gaffan, & Murray (1994) found such a result with monkeys during an object recognition paradigm. Monkeys were presented with a multicolored pattern and trained with food rewards to touch the previously seen pattern when it appeared again. Once trained, they were given a novel set of items to study. After a short delay of either 0, 5, 15 or 30 seconds, the monkeys were presented with a rewarded old pattern alongside an unrewarded novel pattern and were allowed to select only one of the presented patterns. Monkeys who had perirhinal and entorhinal cortices removed were increasingly impaired during this recognition task when the delay between the study and test period increased. A separate study found that these recognition memory impairments were greater with PRC lesions than entorhinal or hippocampal lesions (Meunier, Bachevalier, Mishkin, & Murray, 1993). These combined findings demonstrate that PRC is a critical brain structure for object recognition memory.

The representational-hierarchical theory accounts for the role of PRC in delay-dependent object recognition memory deficits as follows. A model of the theory assumes that during the delay between encoding an object and being tested for memory of it, participants imagine or perceive other visual stimuli in the surrounding environment (Cowell, Bussey, & Saksida, 2006). The model also assumes that all objects in the visual world are composed from a limited pool of visual features, such that when viewing a stream of real or imagined objects, the same features appear repeatedly. Feature-level interference is created when task stimuli share features with those *real or imagined*

objects in the world. Repeated presentation of the commonly occurring features results in all such features appearing familiar, even when they occur as part of a test object that is itself novel. Consequently, at test the representations of the novel object's individual features, housed in posterior visual cortex, appear familiar. If an individual has PRC damage, meaning they must rely upon posterior feature representations, false recognition of a novel object occurs because the new object cannot be distinguished from the old object in terms of familiarity – the features of all objects (including the novel one) appear familiar. The longer the delay period, the greater the feature-level interference experienced and thus the greater the object recognition memory impairment.

The model can similarly explain a second effect found by Eacott et al. (1994): object recognition memory performance deteriorates as list length increases. As more stimuli are presented at study (as list length increases in a memory task), common features repeatedly occur across *items in the list*, increasing the amount of feature-level interference. Feature-level interference causes novel objects with those shared features to appear familiar when a PRC-lesioned participant is forced to rely on familiar simple-feature representations in posterior areas alone. The mechanism by which this feature-level interference impairs recognition memory is the same mechanism by which feature ambiguity impairs perceptual discrimination in PRC-lesioned individuals, as described in the previous section.

In contrast, in the healthy brain, whole-object representations in PRC shield an individual from deficits in an object recognition memory task by forming unique, conjunctive representations. These representations are not vulnerable to visual interference because whole objects are unique and reside within a much larger

‘representational space’ than simple features (i.e., the pool of possible objects is much larger than the pool of possible features). Consequently, a particular object (such as the novel object that appears at test) is very unlikely to be experienced during the delay or to appear elsewhere within the stimuli set. Because the complex, conjunctive object representations residing in PRC are unaffected by feature ambiguity (occurring when task stimuli share features with each other) or feature-level interference (occurring when task stimuli share features with objects in the world), the novel object presented at test always appears novel.

The model assumption that PRC damage forces reliance on simple-feature representations, which are susceptible to perceptual interference, also predicts rodent empirical findings. Rats with bilateral PRC lesions were exposed to two identical objects made of Legos during the sample phase and then were exposed to the same Lego object and a novel Lego object during a choice phase (Bartko, Winters, Cowell, Saksida, & Bussey, 2007a). When the old and novel Lego objects shared many simple features (i.e., similar Lego pieces in similar formations), the lesioned rats demonstrated more object recognition impairments. Specifically, deficits in discrimination between novel and familiar Lego objects were revealed when lesioned rats were not spending more time exploring novel objects, as expected of healthy rats. The representational-hierarchical theory predicts this result because the PRC lesion creates reliance on simple-feature representations that cannot support correct recognition memory or perceptual discrimination between the highly similar stimuli.

The counterintuitive model prediction that novel objects appear familiar after PRC lesions and that this deficit is an effect of perceptual interference was also

empirically tested with rodents. After a study-test delay, PRC-lesioned rats were found to treat novel stimuli as familiar (i.e., reduced exploration periods for novel objects that were similar to exploration periods for familiar objects) (McTighe et al., 2010). However, this recognition impairment was ameliorated when the delay involved visual restriction (i.e., placing the rat in a black box instead of an open bar cage). According to the representational-hierarchal account, restricting visual interference during the study-test delay prevents feature-level interference. This allows novel objects to appear novel on the basis of simple-feature representations, shielding PRC-lesioned animals from the effects of perceptual interference during a delay.

Again, and perhaps most importantly, identical explanations can be used to account for similar findings in humans. Analogous to tasks with PRC-lesioned rodents, Yeung, Ryan, Cowell, & Barense (2013) employed an implicit test of recognition memory with humans at risk for mild cognitive impairment (MCI), a disorder that indicates likely incipient MTL damage (Petersen et al., 2006). Healthy humans show more fixations towards novel stimuli than to previously encountered stimuli; therefore, the number of fixations could be taken as an implicit measure of familiarity that was unaffected by decision criterion (Yeung et al., 2013). Participants first viewed a series of repeating object images in the study phase and then the test phase presented previously viewed objects, novel objects with similar features, and novel objects with dissimilar features. Individuals at risk for MCI treated novel items that shared features with previously studied items as familiar (i.e., exhibited fewer fixations) because the features of the object were made familiar by the studied items. However, novel items that did not share features with the studied items were treated as novel (i.e., elicited more fixations)

because the features of the object remained novel. Again, the representational-hierarchical theory explains this in terms of feature-level interference that causes false recognition of novel objects because – in the case of participants with MCI – recognition judgements are more dependent on simple-feature representations.

Lastly, the restriction of perceptual interference during a delay is also seen to benefit MTL-lesioned patients in object recognition memory tasks. During the study phase, a series of objects were presented during an incidental memory task (Newsome, Trelle, Rowe, Cowell, & Barense, 2014). The study phase was followed by a 10 minute delay that contained 1) minimal interference (sitting in a dark room with eyes closed); 2) visual interference (scrambled versions of the objects); or 3) cognitive interference (completing the Montreal Cognitive Assessment). Similar to McTighe et al. (2010), the minimal visual interference delay condition resulted in improved forced choice object recognition memory at test. Consistent with previous explanations of the model, accurate familiarity judgements can be based on simple-feature representations in MTL-lesioned patients in this condition, because feature-level interference was restricted during the delay and the features of the novel objects therefore remain novel.

1.2 Aims

As seen above, findings from MTL-lesion studies can be explained by three of the representational-hierarchical theory's assumptions: 1) representations in the ventral-visual-medial-temporal-lobe pathway are organized in a hierarchical manner, with more conjunctive representations located toward the MTL; 2) when conjunctive representations are impaired, an individual is forced to rely on more posterior simple-feature

representations; and 3) simple-feature representations may be insufficient for solving certain perceptual and mnemonic tasks when perceptual interference is involved. The current studies propose to gather neural and behavioral evidence in humans to further examine the third assumption outlined above: the effects of interference.

First, although feature-level interference has been shown to cause novel objects to appear familiar in MTL-lesioned animals and humans, as measured with behavioral performance, there is no work that directly examines the effects of interference on *neural representations*. Experiment 1 aims to test whether posterior ventral visual stream representations of novel objects will bear neural signatures of familiarity after feature-level interference in healthy participants.

Second, we wanted to further investigate the effect of interference on a behavioral recognition memory task with a population thought to have compromised anterior representations: older adults with natural structural changes in the MTL. The Deese–Roediger–McDermott (DRM) paradigm is commonly used to assess the effects of interference on memory; however, previous findings about how these effects vary with age and type of interference are conflicting. Experiment 2 will examine whether older adults experience memory impairments from feature-level interference, but are paradoxically shielded from semantic-level interference. Testing both of these predictions will significantly contribute to the body of evidence supporting the representational-hierarchical account.

CHAPTER 2

EXPERIMENT 1

2.1 Testing the Theory with Neural Evidence in Healthy Young Adults

Although behavioral predictions of the representational-hierarchical theory for perception and memory have been investigated, the assumptions of the representational-hierarchical theory regarding the *neural representations that underlie that behavior* have not yet been explored. The representational-hierarchical account assumes that the effect of visual interference on memory (i.e., the false signaling of familiarity by posterior representations) is mediated via the susceptibility of posterior visual representations to such interference. However, the effect of visual interference – specifically, repeated presentation of simple visual features – on posterior visual representations has not yet been examined directly within the framework of the representational-hierarchical theory. Our hypothesis is that posterior regions (which contain simple-feature representations) will bear neural signatures of familiarity after visual interference from stimuli with shared features; however, anterior areas (that contain representations of the unique conjunction of features) will demonstrate signatures of familiarity only when that exact object is repeated. We predict that these signatures of familiarity can be captured by changes in neural activity.

Several studies have shown that when a stimulus is repeated, the neural activity evoked by that stimulus decreases (Grill-Spector, Henson, & Martin, 2006). This response decrease, also known as repetition reduction (RR), has frequently been associated with priming in the perceptual literature, i.e., when the phenomenon is

observed in visual cortical areas (Grill-Spector et al., 2006). However, given that RR effects have also been observed in PRC (Brozinsky, Yonelinas, Kroll, & Ranganath, 2005) and the PRC is important for memory, RR is additionally associated with mnemonic familiarity when it occurs in anterior regions (Brown & Xiang, 1998; Henson, Cansino, Herron, Robb, & Rugg, 2003; Wang, Ranganath, & Yonelinas, 2014).

Assuming that RR is a neural marker of familiarity, we are able to use it as an experimental assay to test whether the neural signatures of familiarity in posterior and anterior regions are consistent with the representational-hierarchical account. Specifically, if an image of a novel object is presented three times, the neural response should decrease from the first (highly novel) presentation to the third (familiar) presentation, such that RR is observed. The RR should occur in both posterior regions assumed to contain feature-level representations and anterior regions assumed to contain conjunctions of features (i.e., whole objects). However, the pattern of RR in these areas will change if the three repeated presentations of a novel object occur *after* a long series of images that depict the same category of object and share simple features (See Figure 2).

The presentation of a series of same-category objects creates visual interference because shared simple-feature representations are repeated with each individual object presentation. These feature representations, stored in posterior regions, are expected to become ‘saturated’ (i.e., reach a maximum) in terms of familiarity. Specifically, the neural response of the first presentation of a novel object (which contains those shared features) at the end of the series already elicits much lower activation than the first presentation of a novel object at the start of the series. As a result, the neural response of

the third presentation of that object at the end of the series shows very little, if any, *further* reduction. In contrast, conjunctive representations in anterior regions should not experience visual interference from a series of same-category objects because the unique whole object is not repeated. Therefore, the neural response in anterior areas does not become saturated and RR occurs as normal from the first to the third presentation of an object at the end of the series.

In addition to the body of research that has demonstrated RR, there has been a small number of studies that have indicated an *increase* in the neural response with stimulus repetition (Dolan et al., 1997; George et al., 1999; Heusser, Awipi, & Davachi, 2013). This repetition enhancement has been linked to a possible secondary process that occurs with repeated targets, but not with initial primes (Henson, 2003), and, within the PRC, better subsequent memory (Heusser et al., 2013). It thus appears that neural signatures of familiarity may manifest as enhancements of neural activity, rather that reductions. Similar to Ezzyat & Davachi (2014), to address this possibility we can evaluate the neural pattern similarity (PS), or the correlation of activation patterns, between the first presentation of an object and the third presentation of an object. This measure allows us to detect changes in neural activation patterns, regardless of the direction.

Moreover, PS provides the added benefits of multivariate pattern analysis (MVPA). MVPA differs from univariate analyses because it examines *patterns* in the BOLD signal *across* voxels, instead of examining the absolute values of BOLD either in individual voxels or averaged across voxels (Haxby et al., 2001; Norman, Polyn, Detre, & Haxby, 2006). MVPA potentially allows for more sensitive tests of a hypothesis than

univariate analyses, because it enables detection of subtle differences in brain activation between experimental conditions that may not be observable in the aggregated estimate of the BOLD signal obtained from averaging over all voxels in an ROI. Ultimately, analogous to the univariate analyses described above, the data can be analyzed to examine the effects of visual interference on anterior and posterior neural representations of first vs. third presentations of an object.

The representational-hierarchical account makes similar predictions for PS as it did for RR (see Figure 2). For both posterior and anterior regions, in the beginning of the series (before any visual interference) the neural pattern of activation should change from the first presentation of an object to the third presentation of that object because the whole object is repeated. This should be exemplified by a lower PS score (i.e., more distinct representations) derived by comparing the patterns elicited by the first and third presentations. However, after visual interference in which simple features are repeated in same-category objects, simple-feature representations in posterior areas become saturated to a point where there is little change between the first and third presentation of a novel object. This will result in higher PS scores (i.e., more similar representations) derived by comparing the first and third presentations at the end of the series. In contrast, representations in anterior regions (such as PRC) do not become saturated because the exact unique conjunction of features is not repeated in the same-category series. Therefore, 'before series' and 'after series' PS scores derived from comparing first versus third presentations should not significantly differ for anterior regions.

2.2 Method

2.2.1 Participants

Twenty-eight participants were recruited from the Dartmouth College community. Five participants were excluded from the analysis because of excessive movement during the fMRI scanning that exceeded a frame displacement threshold of 0.9 for over 10% of the total time points, or because of failing to stay awake during the task. The remaining 23 participants were between the ages of 18 and 32 years old (M = 21.6, SD = 3.3), 18 of which were female. All participants spoke English fluently; had normal or corrected-to-normal vision; no history of neurological illness; and had no contraindications for MRI scanning. Participants gave written informed consent after being informed about the procedures and possible risks of the experiment and were compensated $20 per hour of participation.

2.2.2 Materials

Stimuli were 288 color photographs from 12 different categories of common everyday objects (e.g., teapots, backpacks, vases, belts). Each category had 24 distinct object images and images between categories shared very few if any simple features.

2.2.3 Procedures

Each participant completed eight functional scans. Within each scan run, seventy-two stimuli trials and 16 null trials were shown, totaling 88 trials per run. Visual images were projected with an Epson ELP-7000 LCD projector onto a screen positioned at the head end of the magnet bore. Participants viewed the screen via a mirror on the head coil.

Images were presented one by one, each placed on a grey background. Presentation duration was 1,200 ms, with a stimulus onset asynchrony (SOA) of 800 ms. A white central fixation cross (+) remained on the screen, including during the presentation of a stimulus, except for the duration of null trials. Null trials presented a red fixation dot at the center of a gray background that dimmed at a fixed rate. This dimming rate was occasionally decreased for participants who had difficulty seeing the dot 'flicker'. Null trials provided a behavioral measure of attention and wakefulness and also provided gaps in the sequence of stimuli that allowed for a better estimate of the hemodynamic response function (HRF) for individual events.

Each run followed an event related design where stimulus trials were divided into four sections within a run; each section contained six unique images from a category of objects and these images were presented three times each (see Figure 3). A section transitioned to the next without any marker. The object categories that were selected for each section determined the level of interference during the run. In a high interference run, all four sections randomly sampled six images from the same category of objects (e.g., all stimulus trials would be images of vases). In a low interference control run, the first and fourth section were sampled from the same object category, but the second and third section were sampled from two different filler object categories (e.g., a run would consist of trials of vases, belts, shoes, and then vases again). All participants saw four high interference and four (control) low interference runs.

Several measures were taken to ensure that run type, object category, and stimulus presentation would not introduce confounds. The order of presentation of high and low interference runs was counterbalanced across participants: odd numbered runs were high

interference and even numbered runs were low interference for all odd-numbered participants and vice-versa for even-numbered participants. For each participant, all 12 categories of images were assigned a category condition that determined when the images within that category would be presented; these category conditions included 'high interference' (sections 1 through 4 of high interference runs); 'low interference' (sections 1 and 4 of low interference runs); or 'filler' (sections 2 or 3 of low interference runs). This assignment was counterbalanced across participants to ensure that each object category was assigned to each category condition at an equal frequency throughout the entire study. Additionally, object categories assigned to the high and low interference category condition were not repeated in other runs within a participant's session. The order of image presentations was randomized with constraints preventing an immediate sequence of the second and third presentation, but also preventing sequences without any repeats at all (allowing second presentations immediately following first presentations). Lastly, null trials were inserted randomly with restrictions that prevented their placement between first and second immediate repeat presentations, the immediate repetition of two null trials, and placement after the last image presentation within a run.

All participants completed one practice run outside of the scanner, before scanning took place. A similar sampling process was used to compose one practice run. The practice run consisted of 58 trials: 10 null trials and 48 image presentations. It followed the format of a low interference run (i.e., with a change of category for images seen in the middle of the sequence) and used three object categories that were not seen in any of the study runs. The sequence of the categories did not change between participants. Each section in a practice run consisted of four unique images repeated three

times. The practice run was presented with the same parameters as described above, but was completed on a laptop computer instead of projected on the screen behind the MRI scanner.

2.2.3.1 Task

Participants were asked to discriminate between the object currently on the screen and the object presented immediately prior by pressing response keys associated with "Same" or "Different". They were instructed to respond at their own pace while the stimulus was on the screen and to be as accurate as possible. When a null trial occurred, participants were told to hit either response key whenever the red dot appeared to flicker. Participants did not need to respond during trials immediately after a null trial or at the beginning of a run. Participants first practiced the task outside of the scanner on a laptop computer and used keys on a keyboard to mark their "Same" and "Different" responses. In the scanner participants responded with button box presses.

2.2.3.2 Functional Localizer

In order to localize brain regions of interest (ROIs) within the ventral visual stream, including lateral occipital cortex (LO), each participant completed two functional localizer scans. During these runs, participants were instructed to passively view a series of images that contained black and white photographs of houses, faces, objects or scrambled objects overlaid with a gray outlined grid. Each run contained 12 blocks and each block belonged to one of the four possible image categories. The sequence of the first four blocks was randomized and this sequence was repeated twice more for each participant. Block duration was 10,000 ms with a 10,000 ms rest period in between

blocks. Within each block, ten stimuli of that block's image category were presented for 700 ms each with a rest period of 300 ms; images did not repeat in other same-category blocks. A black dot encircled by a black outline served as a fixation point both during image presentation and rest period.

2.2.3.3 Image Acquisition and Preprocessing

Scanning was performed on a Phillips Intera Achieva 3T scanner (Philips Medical Systems, Andover, MA) equipped with a thirty-two-channel SENSE head coil, at Dartmouth Brain Imaging Center, Hanover, NH. Whole-brain anatomical images were acquired first using a T1-weighted MP-RAGE sequence (160 sagittal slices; TR, 9.9 ms; TE, 4.6 ms; 8 flip angles; 1 x 1 x 1 mm voxels). Functional images were then acquired using a T2-weighted, Quasar dual high performance gradient sequence (TR, 2000 ms; TE, 30 ms; flip angle, 90°; FOV, 240 mm; 3x 3 x 3 mm voxels). Thirty-five axial slices were acquired during each functional run. Experimental functional runs had 159 volumes and functional localizer runs had 125 volumes.

The data were preprocessed and analyzed with BrainVoyager QX software, in conjunction with custom MATLAB scripts for analyzing functional time-series data. Functional data were coregistered to anatomical scans, slice-time corrected, motion-corrected, temporal high-pass filtered (5 cycles/run), and transformed into Talairach space. For univariate analyses, the functional data were additionally spatially smoothed using a 6 mm Gaussian kernel. Functional timecourses within each run were normalized (Z-scoring).

2.2.3.4 Definition of Regions of Interest

For posterior brain regions in visual cortex (LO), the ROI was defined using the data from the Face-House-Object-Scrambled functional localizer. LO was selected by creating a Statistical Parametric Map (SPM), thresholded for 4 or more contiguous voxels passing $p < 0.05$, from a random effects general linear model (GLM) that contrasted object stimulus presentations with scrambled stimulus presentations. A sphere (radius 6mm) was placed in each hemisphere on the voxel with peak group-level activation for an 'objects greater than scrambled' contrast. Peak voxels were confirmed to be located at similar Talairach coordinates as those found in the literature.

For anterior brain regions (PRC), the ROI was anatomically defined for each participant using landmarks as described by Pruessner et al. (2002). In all analyses, data from left and right hemispheres were combined into a single ROI.

2.2.4 Statistical Analysis

2.2.4.1 Repetition Reduction Analysis

To examine the effects of repetition and visual interference on neural activity, trials were binned by repetition (first, second-immediate repeat, second-non-immediate repeat, and third), section of presentation series (first, second, third, and fourth), and interference type (high and low). Estimates of the BOLD response in each ROI were obtained using a GLM that contained separate regressors for each condition of interest, as well regressors for motion. Each regressor combined a boxcar model of the stimulus time-series (0 when stimulus absent, 1 when stimulus present) with a canonical HRF. The

resulting beta weights from the GLM were averaged across all voxels in an ROI, for each participant, to give estimates of the BOLD response for each ROI.

For each stimulus, RR was calculated by subtracting the estimated BOLD response (i.e., the mean beta weight in an ROI) of the third presentation from the first presentation of that object. The average RR for each condition of interest, collapsed across trials and participants, served as the dependent variable for a 2 x 2 x 2 repeated-measures analysis of variance (ANOVA). The ANOVA included the following factors: (1) Section, 1 and 4; (2) Interference, high and low; and (3) ROI, LO and PRC.

We expected a three-way interaction between Section, Interference, and ROI. Additional planned comparisons that examine RR for each ROI, separately, were predicted to reveal no significant effects of Interference or Section, and no interaction of Interference and Section in PRC (an anterior brain region with unique conjunctive object representations). More precisely, in PRC, on either high or low interference runs, RR was not expected to be significantly different from section 1 to section 4. However, within LO (a posterior brain region hypothesized to represent collections of simple visual features rather than complex object wholes), we expected a significant effect of Interference and a significant interaction between Interference and Section. In this region, RR was predicted to be greater for section 1 than section 4 during high interference runs, but not to be significantly different during low interference runs.

2.2.4.2 Pattern Similarity Analysis

To examine the effects of repetition and visual interference on the similarity between neural activation patterns, a separate GLM was estimated for each trial of the

experiment, regardless of condition (Ezzyat & Davachi, 2014; Mumford, Turner, Ashby, & Poldrack, 2012). Each of the trial-GLM's contained one regressor for the trial, one regressor for all remaining trials (n-1), and motion regressors. These experimental regressors were modeled with the same boxcar function method as described above. The model provided activation pattern estimates for every voxel within an ROI for each trial of interest. Estimates of the single-trial activation patterns were then extracted in pairs of first and third presentations of a specific object in sections 1 and 4, and during high and low interference runs. Skipped correlation, which is robust to outliers, was then used to find the strength of association between these pairs of estimates (see Pernet, Wilcox, & Rousselet, 2013 for further detail on robust correlation). The resulting correlation (r) values then underwent Fisher's z-transformation and were averaged within each subject before being used as a measurement of PS in the final analyses.

PS scores were first analyzed in a three-way (2x2x2) ANOVA. The three factors were (1) Section, 1 and 4; (2) ROI, LO and PRC; and (3) Interference, high and low. We expected to see a significant interaction of Interference, ROI and Section. To further investigate this interaction, the difference in PS scores between section 1 and section 4 (Section 1_PS – Section 4_PS) served as the dependent variable in a 2x2 ANOVA with ROI and Interference as factors. This provided a measure of the effects of interference on neural activation pattern changes that signal familiarity.

According to our predictions, neural representations change as they become familiar (i.e., the neural patterns of the first and third presentation of an object should be dissimilar). We expected this dissimilarity to be present in section 1 (before interference), regardless of run type, for both LO and PRC because both simple-feature and whole

object representations become familiar with repeated presentations of an object. However, in section 4 (after high levels of visual interference in which simple features were repeated in same-category objects), simple-feature representations in LO are expected to become saturated to a point where there is little change between the first and third presentation of a novel object with those shared features (i.e., the neural patterns of the first and third presentation of an object should be similar). This effect in LO during high interference runs is expected to manifest as a negative Section 1_PS – Section 4_PS score (i.e., greater PS scores in Section 4 than Section 1).

In contrast, when there is limited or no effect of feature-level interference in LO (i.e., presentation of different-category objects), simple-feature representations do not become saturated and representations change as they did in section 1 (i.e. neural patterns of the first and third presentation of an object are dissimilar). Thus, during low interference runs in LO, the Section 1_PS – Section 4_PS score is expected to be small, or near zero, (i.e., limited difference between Section 4 and Section 1 PS scores). Similarly, the Section 1_PS – Section 4_PS score is expected to be small, or near zero (i.e., little difference between Section 4 and Section 1 PS scores) for both high and low interference runs in PRC. Because PRC stores whole object representations that are resistant to feature-level interference, PRC representations do not become saturated. Thus, representations change between the first and third presentation of a novel object in section 4 in a similar manner as in section 1 (i.e., dissimilar neural patterns for the first and third presentation of an object).

2.3 Results

2.3.1 Behavioral Performance

As indicated by 0% accuracy on several runs, five participants reversed the response keys associated with "Same" or "Different" during the discrimination task. Their responses were corrected before any further analysis and the mean accuracy for these participants improved dramatically (average mean accuracy increase of 93.51%). The average accuracy on all trial types was 94.59%, with a mean accuracy of 82.47% and 96.04% on same and different trials, respectively. Participants were awake and successfully completing the incidental task.

2.3.2 Repetition Reduction Analysis

Contrary to our predictions, the three-way ANOVA of RR did not reveal a three-way interaction between Section, Interference, and ROI, F (1, 22) = 0.23, p = .64 (see Figure 4). In PRC, there were no main effects of Interference, F (1, 22) = 0.83, p = 0.37, or Section, F (1, 22) = 0.29, p = 0.60, and no interaction between Interference and Section, F (1, 22) = 0.74, p = 0.40. Additionally, in LO there were also no main effects of Interference, F (1, 22) = 0.53, p = 0.47, or Section, F (1, 22) = 0.25, p = 0.62, and no interaction between Interference and Section, F (1, 22) = 0.1.14, p = 0.30. In LO, although not statistically different, the mean RR was greater for section 4 than section 1 during high interference runs and greater for section 1 than section 4 during low interference runs. Similarly, in PRC the mean RR was greater for section 4 than section 1 during high interference runs, but did not reach significance. The mean RR between

section 1 and 4 during low interference runs in PRC did not differ. It appears that RR was occurring to a minor extent, but was not affected by visual interference as expected.

2.3.3 Pattern Similarity Analysis

A three-way ANOVA of PS demonstrated a main effect of ROI, F (1, 22) = 68.8, p <.001 and, consistent with our prediction, a trending interaction of Interference, Section, and ROI, F (1, 22) = 3.85, p = 0.06 (see Figure 5). None of the other main effects or lower order interactions were significant (p > .05). Investigation of this interaction with Section 1_PS – Section 4_PS score as a dependent variable revealed no significant effects (see Figure 6). However, when examining the trends of Section 1_PS – Section 4_PS scores, we found that within LO the Section 1_PS – Section 4_PS score was greater for low interference runs than high interference runs and that the Section 1_PS – Section 4_PS score for the high interference runs was negative, as predicted. Though, this Section 1_PS – Section 4_PS score was numerically negative, it was not significantly different from zero and so it does not clearly indicate that there was more PS in section 4 after visual interference than in section 1. Within PRC, the Section 1_PS – Section 4_PS score was greater during high interference runs than low interference runs and the Section 1_PS – Section 4_PS score was negative during low interference runs, but not significantly different from zero. All Section 1_PS – Section 4_PS score effects were not significant and thus conclusions cannot be made from these numerical trends.

2.4 Discussion

Experiment 1 tested whether posterior visual cortex, assumed to contain simple-feature representations, would demonstrate neural signatures of familiarity for novel

objects after exposure to simple-feature interference. Both LO and PRC were predicted to have signals of familiarity (RR or PS) for repetitions of an object. However, after interference from same-category objects, we predicted simple-feature representations in LO would demonstrate saturated signals of familiarity for a novel object's first presentation. This saturation was expected to occur because shared simple features were repeatedly presented within the same-category object series, and thus should appear familiar. This post-interference saturation of familiarity was not predicted to occur in PRC, because PRC contains unique conjunctions of simple features that would not be repeated in the same-category object series. This study did not confirm nor refute this prediction. The first analysis of RR did not demonstrate any effect of the visual interference manipulation nor ROI differences. In the second PS analysis, there was a trend of our predicted effect in LO (i.e., greater PS after visual interference), but this was ultimately not statistically significant.

The current nonsignificant results may reflect study limitations or other artifacts. For instance, analyses could be underpowered because of a small final sample size (n = 23) after excluding several participants with excessive movement. Some researchers claim that trends towards significance may pass the alpha threshold and become significant after further data collection. However, this claim is often misleading as additional data may reveal even greater *p*-values than those in the current study (Wood, Freemantle, King, & Nazareth, 2014). The study may also be affected by distortion and signal loss typical of the medial temporal lobe in fMRI studies (Olman, Davachi, & Inati, 2009), or signal loss in mid-to-posterior ventral visual regions experienced in our datasets

collected on this particular scanner. The former would affect neural activity recorded from PRC, and the latter would impact signals from LO.

Another possibility is that the nonsignificant results are attributable to the stimuli used in the experiment. Our study predictions were largely based on an assumption about the stimuli: diverse objects within the same category share several simple features. The overlap of simple features between objects was expected to cause visual interference and neural signatures of (false) familiarity in regions containing simple-feature representations. Although this assumption seems plausible intuitively, it could be that the stimuli were in fact not similar enough to elicit RR and PS responses from non-identical objects. Future work should manipulate the degree of similarity between stimuli in a systematic way to address this possible issue.

CHAPTER 3

EXPERIMENT 2

3.1 Testing the Theory with Behavioral Evidence in Aging Populations

Our hypothesis is that behavioral studies with healthy older populations will demonstrate cognitive impairments that fall on a spectrum between healthy young adults (without deficits) and patients with MTL damage. According to the representational-hierarchical account, these cognitive impairments will arise from the same mechanisms as postulated for individuals with MTL damage, namely compromised conjunctive representations in the MTL. This is because many of the structural changes that occur with normal aging affect the MTL (Raz, Rodrigue, Head, Kennedy, & Acker, 2004; Wang et al., 2002). As a result of these changes, older populations experience deficits in their memory that are self-reported and empirically supported (Craik, 2008; Light, 1991).

This impairment has been demonstrated in the DRM paradigm (Deese, 1959; Roediger III & McDermott, 1995). During study, participants are presented with a series of words from several different lists. On a given list, all words are semantically related to a non-presented prototype word. At test, participants commonly report that the related prototype word was seen, although it was never presented. These false alarms, or false memories, occur much more frequently for older adults (Dennis, Kim, & Cabeza, 2008; Norman & Schacter, 1997) and adults diagnosed with MCI and Alzheimer's disease (Balota et al., 1999). Some researchers have argued that older adults rely more on semantic gist – the general meaning of the experience – to make recognition decisions (Koutstaal & Schacter, 1997; Tun, Wingfield, Rosen, & Blanchard, 1998). It has

subsequently been debated whether false alarms in this population occur because activation spreads between semantically related words (either at time of encoding or at time of retrieval), rendering the non-presented prototype words familiar and leading to source misattributions (Roediger III, Balota, & Watson, 2001) or because shared semantic gist traces are retrieved instead of verbatim traces (Brainerd & Reyna, 2001; Reyna & Brainerd, 2002). The representational-hierarchical theory provides an alternative to both of these explanations, and makes a novel prediction for the DRM paradigm.

According to the representational-hierarchical framework, false memories for older populations occur in the DRM paradigm because of compromised conjunctive representations in anterior regions such as the MTL. Conjunctive representations are proposed to be impaired in older populations because of structural changes within the MTL. We suggest this impairment affects both representations of the conjunctions of features that correspond to whole objects (located in the PRC) and associative conjunctions, such as semantic knowledge that is associated with objects, or the relationship between objects and their context, in other anterior structures like lateral anterior temporal lobe or hippocampus (Hsieh, Gruber, Jenkins, & Ranganath, 2014; Nielson, Smith, Sreekumar, Dennis, & Sederberg, 2015; Schmolck, Kensinger, Corkin, & Squire, 2002).

Similar to other accounts of the DRM effect such as the activation-monitoring and fuzzy trace theories (Reyna & Brainerd, 2002; Roediger III, Balota, et al., 2001), the representational-hierarchical theory assumes that healthy young adults make false alarms in the standard DRM paradigm because the exemplar words on a list are conceptually or

semantically associated with the non-presented prototype word. The semantic associations cause a novel prototype word that is associated with the studied words to appear familiar because it was activated through association either at time of study or at time of test. However, this semantic interference (which produces a false sense of familiarity) must be constructed (or inferred) by the participant, regardless of their age, by allowing activation of the studied words to associatively activate the non-presented prototype.

We propose that the representations of associative relationships in anterior temporal regions are partially compromised in older adults, relative to young adults. In the standard DRM paradigm, in which each semantic list is presented in isolation and tested before moving on to the next list, older adults (like young adults) can nonetheless extract the associative relationship between list items (leading to semantic interference and later false alarms for related, unstudied items). However, owing to compromised conjunctive representations in older adults, the extracted associative relationship is bound more poorly to the context (i.e., the fact of experiencing the information in the study phase of the experiment), which produces a higher rate of false alarms than in young adults because contextual information cannot readily be used to prevent endorsement of associated items that were not studied.

These predictions change when the DRM paradigm is modified (see Figure 7). The current study will use a DRM paradigm in which semantic DRM lists are intermixed with each other, or with perceptually related DRM lists (thus juxtaposing items that bear no semantic relation). We predict that in this paradigm – in which the semantic relationships between the studied items are harder to extract – older adults may be less

susceptible to false recognition because they will fail to extract the associative semantic relations that cause semantic interference. An older participant will have more difficulty extracting the associative semantic relations between items because they are not as obvious when stimuli from different lists are intermixed and because older adults are hypothesized to possess compromised representations of semantic and contextual associations. When older participants do not suffer semantic interference from associative semantic relations, novel semantically related words will not receive the spreading activation from the old semantically related word. As a result, these novel words will less often be mistaken as familiar and there will be fewer false alarms. In contrast, young participants may still be able to extract the semantic associations present among items, even when the associations are not as easy to extract, because they have unimpaired representations of semantic relations. Consequently, young adults will continue to suffer from semantic interference and make false recognition judgements of novel semantic words in this modified DRM paradigm.

In the arguments laid out above, an older adult's reduced false alarm rate will occur only if the interference that negatively impacts familiarity discrimination is caused by semantic associations. If a DRM list contains words that are all perceptually similar, such as words that are phonemically and orthographically similar, false alarm rates will be higher in older adults than in young adults. This occurs because the perceptual interference between exemplar words and novel prototype words resides at the simple feature level. Consequently, this interference is present in the stimuli; it does not need to be extracted, but instead is readily available for all participants to experience, whether or not their anterior, conjunctive representations are compromised. Older adults, whose

impaired conjunctive representations should shield them from semantic interference in the modified DRM paradigm, we propose will now demonstrate difficulties resolving the simple-feature interference in the perceptually similar condition. In the absence of intact conjunctive representations, older adults must rely on simple-feature representations for familiarity discriminations when there is high feature-level interference. This results in more false alarms in older adults for novel words that share overlapping perceptual features with the studied items. Young adults may also have false alarms caused by simple-feature interference, but to a lesser degree than older participants because they are able to resolve the interference using their intact conjunctive representations.

3.2 Methods

3.2.1 Participants

A total of 120 participants were recruited from the University of Massachusetts-Amherst and the local community, including 40 older adults and 80 young adults. One older adult was excluded before analysis because Matlab quit unexpectedly during the study phase. A further six subjects were excluded during analysis (see Section 3.2.4.1: Signal Detection Model). Of the remaining participants, older participants were between the ages of 60 and 92 years old (M = 71.4, SD = 7.3) and young adults were between the ages of 18 and 30 (M = 20.7, SD = 2.7). All participants spoke English fluently; had normal or corrected-to-normal vision; and were in general good health with no history of psychiatric or neurological conditions. Participants gave written informed consent after being informed about the procedures of the experiment. Undergraduate students were

compensated one extra credit that could be applied to an undergraduate psychology class and non-students were compensated $10 per hour of participation.

3.2.2 Materials

The study adapted materials from Shiffrin, Huber, & Marinelli (1995). Stimuli consisted of 25 lists that were composed of 11 exemplar words and one prototype word (see Appendices A, B, and C for complete stimuli set). Fifteen of these lists contained words that were all semantically similar within the list and tended to be relatively long (5-14 letters) with relatively low natural language frequency. The other ten lists contain words that were either phonemically or orthographically related to the prototype word and were either three-letter or four-letter monosyllabic words with a high natural language frequency. Although the two lists were not matched in word language frequencies, previous research has shown that word frequency does not affect false memory (Roediger III, Watson, McDermott, & Gallo, 2001; Sherman & Jordan, 2011). Further, word length has only been found to affect false memory when the length of critical lures differs from the length of within-list words, which did not occur in this paradigm (Madigan & Neuse, 2004). In addition to the words on these lists, there were 44 extra semantic and 20 extra phonemic/orthographic words that met the same criteria as the words on semantic and phonemic/orthographic lists (i.e., language frequency and word length), but were not exemplars to any of the prototypes (i.e., they were unrelated extra words). No words were offensive, emotionally loaded, or otherwise provocative.

3.2.3 Procedures

The experiment consisted of two phases: a study phase with 120 words and a test phase with 144 words. Both phases were completed on a desktop computer with a separate monitor or on a laptop computer. During the study phase, eight or two exemplars from each of the lists, ten semantic and ten phonemic/orthographic, were presented for three seconds each. The selection of ten semantic lists, out of a total possible 15 semantic lists, for use in the study phase was counterbalanced across participants. Additionally, we randomized for each participant which lists had eight exemplars or two exemplars presented; the specific exemplar words presented; and the order of presentation during this phase. Consequently, semantic and phonemic/orthographic stimuli were intermixed. Ten extra semantic words were presented at the beginning and end of the study list to prevent recency and primacy effects in the test phase. All words were presented in a white font on a black background.

Once the study phase was completed, the test phase began without any delay. The test list contained, in a randomized order for each participant, twenty extra semantic words, twenty extra phonemic/orthographic words and, from each of the 20 study lists, two studied exemplar words (targets), two non-studied exemplar words (related lures), and one prototype word (critical lure). Again, semantic and phonemic/orthographic stimuli were intermixed. No practice phase occurred before the test phase because the four remaining extra semantic words served as buffer practice trials before the trials that contained list words during the test phase. The other extra words inserted into the test phase (twenty semantic and twenty phonemic/orthographic) were included as distractors (unrelated lures) to measure false memory for words that did not belong to any list and

had no interference. A participant's response cued the next presentation of a word, so participants could take as long as needed to make a familiarity decision on each trial.

3.2.3.1 Task

At the beginning of the experiment, participants were informed that some words presented during the study phase will be repeated during the test phase and that there will be a final recognition memory test. Additionally, in an attempt to prevent the semantically and phonemically/orthographically related words from appearing strange or distracting, participants were informed that many of the words they were to see would seem similar or related. During the study phase participants were asked to rate the pleasantness of the presented word by pressing keys numbered 1-5. On this 5-point scale, 1 was considered very pleasant, 5 was very unpleasant, and 3 was neutral. In the test phase, participants were prompted to give a rating of their confidence that the current word was seen before. This confidence was measured on a 6-point scale where pressing 1 meant that he/she was very sure the item was a new word and pressing 6 meant that he/she was very sure it was an old word.

3.2.3.2 Neuropsychological Tests

All of the older adult participants completed an additional one-hour neuropsychological battery after the experiment to assess cognitive abilities and to confirm their healthy cognitive status. These tests assessed memory, thinking, language, and visual perception and included Wechsler Memory Scale-IV Logical Memory I & II; Trails Making Test Parts A and B; Wechsler Adult Intelligence Scale-IV Digit Span; Mini-Mental State Examination; and Visual Object Space Perception Silhouettes.

3.2.4 Statistical Analysis

3.2.4.1 Signal Detection Model

A signal detection theory (SDT) model was selected to fit the results. SDT models assume that a participant's response is based on a combination of the degree of discriminability - in this context, the ability to detect whether a word was previously studied - and a criterion value, which governs the participant's decision rule (Macmillan & Creelman, 2005). In this model, on any given trial a participant must make an old-new recognition decision based on a sampled familiarity value for the current word. Familiarity values are assumed to vary from trial to trial according to a normal distribution (see Figure 8) and each type of word (e.g. target, lure, etc.) has a separate probability distribution. The likelihood of a particular response (e.g., a hit or false alarm) is determined from the area under the curve to the left or right of the criterion value.

Typically, targets, or previously seen words, have a greater mean familiarity value than lures and so the familiarity distribution for targets is shifted to the right; however, some ambiguous familiarity values, where the target and lure familiarity distributions overlap, will remain. Discriminability (d') is the difference between the mean familiarities for the target and lure distributions. When a participant has a greater d', there will be less overlap between the two distributions; it is unlikely that the distribution would not overlap at all (a participant with perfect recognition performance). Responses made in this ambiguous decision space are of particular interest.

In order to make a recognition decision in the decision space, participants must employ a criterion (*k*). Any familiarity value above *k* elicits an "old" response and any value below *k* elicits a "new" response. This leads to four possible response types: 1) hits

(H) when the word is old and the response is old; 2) false alarms (FA) when the word is new and the response is old; 3) misses (M) when the word is old and the response is new; and 4) correct rejections (CR) when the word is new and the response is new. To calculate d' values, it is sufficient to know the frequencies of hits and false alarms, along with total number of target and lure trials. This is because the proportion of misses and correct rejections is simply one minus the proportion of hits and false alarms, respectively. The rates of hits and false alarms can be calculated by the proportion of area under the target distribution curve to the right of *k* and the area under the lure distribution curve to the left of *k*, respectively. Therefore, d' and *k* provide a complete description of a participant's recognition performance, including their hits and false alarms. Assuming *k* is fixed to zero, a d' value of zero would produce 50% hits and false alarms (i.e., chance performance). As d' increases, the percentage of hits would increase, and the percentage of false alarms would decrease.

The model used here included three distributions per each of the four word conditions. The three distributions were for each word type: targets, critical lures, and related lures. The four conditions consisted of list type (semantic or phonemic/orthographic) and list length (2-item or 8-item). In addition, there was one unrelated lures distribution that did not vary by list type nor list length. The six confidence ratings were collapsed into a dichotomous response (old-new, in which responses 1-3 were mapped to 'new' and responses 4-6 were mapped to 'old') because an insufficient number of participants used the full scale when responding (see Figure 9); consequently, the model assumed variance equal to one. Lastly, the criterion *k* was assumed to be fixed across all conditions because the words were randomly presented as

one long list, not blocked into separate lists based on condition. This presentation structure makes it unlikely that a participant would be aware of the condition of a word and subsequently shift his/her *k* for that specific condition. Therefore, a total of 13 values were calculated for each participant: for each of the four possible combinations of list length (2-item or 8-item) and list type (semantic or phonemic/orthographic), d' between related lures and unrelated lures; d' between critical lures and unrelated lures; d' between targets and unrelated lures; and one fixed *k* parameter across all conditions.

The values of the signal detection model were derived from algebraic formulas. First, we identified subjects whose average accuracy across conditions was significantly lower than chance (0.42; n = 4) and flipped their old/new responses, assuming that these participants had accidentally switched their key responses during the experiment. Any subject whose average accuracy still remained within a 95% confidence interval around chance performance (0.42-0.58) was removed from the analysis (n = 6). We then applied the Snodgrass-Corwin correction for instances of low frequency responses (i.e. hit rates of 1.0 or false alarm rates of 0.0) by adding .5 to the response count and 1 to the number of old or new trials (Snodgrass & Corwin, 1988). For each participant, the fixed *k* was calculated in respect to the corrected false alarm rate for unrelated lures ($k = -[z(\text{FA rate})]$) and then d' values were calculated in respect to this *k* value ($d' = z[p(\text{old})] + k$).

In our analyses, the discriminability between critical lures and targets and the discriminability between related lures and targets were of primary interest (not the d' between unrelated lures and other distributions), and yet because we calculated the d' values by fixing *k* in relation to the unrelated lure distribution, all d' values were calculated in reference to unrelated lures. To obtain the d' values of interest, we

subtracted the appropriate calculated d' values from each other. That is, within each condition and for each participant, we subtracted the d' between critical and unrelated lures from the d' between targets and unrelated lures (to give d' for the discriminability of critical lures and targets) and the d' between related and unrelated lures from the d' between targets and unrelated lures (to give d' for the discriminability of related lures and targets). Figure 10 illustrates how this subtraction provided d' values of interest for a given condition.

Additionally, the list length condition simply served to index the extent to which any observed false memory for related lures is induced by mnemonic processes (i.e., by studying a list of related items) rather than being produced by inherent properties of the kinds of words that are selected as members of related lists in the DRM paradigm. For example, if we looked at d' scores for only 8-item lists, discriminability could be impaired because the word that always serves as the critical lure (and thus has certain qualities of frequency, initial familiarity, etc. that allow it to relate to all other words on the list) is more prone to be falsely remembered, or because the semantic lures are inherently different from phonemic/orthographic lures (e.g. all semantic lures within a list have a backward association strength, while phonemic/orthographic lures do not), regardless of the interference built up by presentation of lures during the study phase. However, these inherent word properties should be present on both list lengths and therefore their effects can be controlled for when we calculate the difference between the d' scores of interest for 8-item and 2-item lists. This set of d' difference scores (d'2 – d'8) not only addresses concerns of inherent word/list property effects, but also can be

considered a measurement of study-related interference (i.e., the effect of seeing more related lures) on recognition performance.

3.2.4.2 Univariate Analysis

First, discriminability (d') scores were analyzed in a four-way (2x2x2x2) ANOVA. The four factors were (1) Age, older and young adults; (2) List Type, phonemic/orthographic and semantic; (3) Item Type, critical lures and related lures; and (4) List Length, 2-item and 8-item lists. In addition, we also examined d' scores for 2-item lists separately (ignoring 8-item list d' values), which allowed us to compare our results with a similar study.

Ly, Murray, & Yassa (2013) found that older adults were selectively impaired by perceptual interference, but not semantic interference for one-item lists. The authors measured the effect of interference on a behavioral assay of pattern separation (i.e., the normalized lure discrimination index calculated as z[p("New"|Lure) – p("New"|Target)]). Because the current study was framed in SDT, we measured the effect of interference on d' between targets and related lures. Although these two measurements were different, we expected similar results as those in Ly et al. (2013): older adults should paradoxically be shielded from semantically-mediated false memories within this modified DRM paradigm.

Second, the d' difference score (d'2 – d'8) was the dependent variable measuring study-related interference in a three-way (2x2x2) ANOVA. The three factors were (1) Age Group, older and young adults; (2) List Type, phonemic/orthographic and semantic; and (3) Item Type, critical lures and related lures. According to the representational

hierarchical account described above, older adults were expected to be shielded from study-related interference for recognition of semantic words, but suffer from more interference for recognition of phonemic/orthographic words, when compared to young adults. This prediction would manifest as an interaction between Age and List Type; specifically with older adults having smaller d'2 – d'8 than young adults in the semantic condition, but a larger d'2 – d'8 in the phonemic/orthographic condition for both related and critical lures.

3.3. Results

3.3.1 Neuropsychological Test Performance

Results of the neuropsychological battery are shown in Table 1. Older adults demonstrated intact group performance on all cognitive tasks with average performance within the normal range relative to established norms or within established passing cutoff scores. Individually, all participants included in the analysis passed the experiment's inclusion criteria of a score greater than 25 on the Mini-Mental State Examination.

3.3.2 ANOVA Results

The first ANOVA with d' as the dependent variable revealed main effects of Age Group, F (1, 111) = 5.06, p = .026, List Type, F (1, 111) = 9.28, p = .003, Item Type, F (1, 111) = 164.8, p < .001, and List Length, F (1, 111) = 28.76, p < .001 (see Figure 11). Additionally, there were significant interactions between Age Group and List Type, F (1, 111) = 5.93, p = .016; List Type and Item Type, F (1, 111) = 6.52, p = .012; and Item Type and List Length, F (1, 111) = 18.9, p < .001. We followed this analysis with two

additional 2x2x2 ANOVA's that examined critical lures and related lures separately to assist with interpretability.

For critical lures, we found main effects of Age Group, F (1, 111) = 7.49, p = .007, and List Length, F (1, 111) = 41.49, p< .001. Younger adults' d' scores were greater than older adults' d' scores and the d' scores for lists composed of only two related items were greater than the d' scores for lists composed of eight related items, as would be expected by the greater level of interference introduced for 8-item lists. There was also an interaction between Age Group and List Type, F (1, 117) = 4.36, p = .04, such that older adults had greater phonemic/orthographic d' scores than semantic, while young adults had greater semantic d' scores than phonemic/orthographic.

For related lures, there were main effects of List Type, F (1, 111) = 16.85, p < .001, with semantic d' scores greater than phonemic/orthographic d' scores; and List Length, F (1, 111) = 6.35, p = .01, with 2-item d' scores again being greater than 8-item d' scores. There was also an interaction between Age Group and List Type, F (1, 111) = 4.35, p = .04, with a similar pattern as seen in critical lures; and a three-way interaction between Age Group, List Type, and List Length, F (1, 111) = 5.15, p = .025. For older adults, d' scores differed numerically less between 2-item lists and 8-items lists for semantically related lists than for phonemically/orthographically related lists (although a t-test did not reveal a significant simple main effect within the 'older' group). However, for young adults, d' scores differed numerically *more* between 2-item lists and 8-item lists for semantically related lists than for phonemically/orthographically related lists. This implies that d' scores for older adults tended to be more influenced by perceptual interference than semantic, whereas for young adults the reverse was true.

For ease of comparison with the results from Ly et al. (2013), which used only lists that were one-item long and examined raw d' scores (rather than d' difference scores derived from two separate list-length conditions), we examined the effects of Age Group and List Type on d' for related lures from only 2-item lists. An ANOVA revealed a main effect of List Type, F (1, 111) = 14.44, $p < .001$, with greater d' scores for semantically related lists; and an interaction between List Type and Age Group, F (1, 111) = 10.99, p =. 001. There was no significant difference between older and young adults' d' scores on phonemically/orthographically related lists, $p = .79$; however, the d' scores of older adults on semantically related lists was significantly smaller compared with young adults, $p = .003$ (see Figure 12). This result differs from the Ly et al. (2013) finding where older adults were impaired on phonemically/orthographically related lists when compared with young adults, but did not significantly differ on semantically related lists (for a potential explanation for this discrepancy, see section 3.4: Discussion).

Lastly, an ANOVA with d'2 – d'8 as the dependent variable revealed a main effect of Item Type, F (1, 111) = 18.9, $p < .001$ (see Figure 13). Again, d'2 – d'8 serves as a measure of study-related interference (i.e., the effect of seeing more related lures) on recognition performance. Because we found a significant difference between critical and related lures, we analyzed them separately. For related lures, there was a significant interaction between Age Group and List Type, F (1, 111) = 5.15, $p = .025$. Although the simple main effects (i.e., group differences for each item type) were not significant, older adults tended to have greater d'2 – d'8 scores than young adults for phonemically/orthographically related lists and young adults tended to have greater d'2 – d'8 scores than older adults for semantically related lists. Additionally, for semantically

related lists, older adults' d'2 – d'8 scores did not differ significantly from zero, t (36) = 0.18, p = .86, but young adults' scores did, t (75) = 2.91, p = .005. That is, older adults were not impaired by an increase in semantic interference, but young adults were. Although these two results cannot be taken as evidence that young and older adults differed from each other on semantic lists, they are nonetheless instructive about the nature of the interaction between Age Group and List Type. For phonemically/orthographically related lists, neither d'2 – d'8 scores from older adults, t (36) = 1.77, p = .085, nor young adults, t (75) = 0.20, p = .84, significantly differed from zero. Again, although simple main effects were not significant, it is informative to note that the numerical pattern seen in phonemically/orthographically related lists was in the opposite direction from that seen in semantic lists, which presumably contributed to the overall interaction that was observed. For critical lures, there were no significant effects, although similar patterns (older adults with greater d'2 – d'8 scores than young adults for phonemically/orthographically related lists and young adults with greater d'2 – d'8 scores than older adults for semantically related lists) can be seen.

3.4 Discussion

Experiment 2 tested (1) whether older adults, compared to young adults, would be shielded from study-related interference for recognition of semantically related words, and (2) whether older adults, compared to young adults, would have worse recognition performance for phonemically or orthographically related words after study-related interference. We expected the first result because semantic interference would be difficult to extract and older adults are assumed to have impaired associative representations. We

expected the second result because simple-feature interference is inherent in the stimuli and we assumed that older adults have impaired conjunctive representations. The study did confirm these predictions for related lures. We found an overall interaction in the direction predicted. This implies that perceptual interference drove young and older adults' scores in the opposite direction than semantic interference. It is important to note that older adults were not globally impaired by interference (i.e., no main effect of Age group in the d'2 – d'8 analysis), but rather they had a different pattern of susceptibility to interference. And further, this specific pattern is supported by the representational-hierarchical account. Critical lures showed a similar numerical trend that was ultimately nonsignificant.

This is different from the results found in previous literature whereby older adults have impaired performance on both phonemically/orthographically and semantically related lures when compared to young adults (Balota et al., 1999); or have selective impaired performance for phonemically/orthographically related lures, but similar unimpaired recognition performance for semantically related lures, when compared to young adults (Ly et al., 2013). Further, when the analyses are specified to closely mimic previous work by Ly et al. (i.e., looking at only the effects of Age Group and List Type on d' of 2-item lists), the results are diametrically different. Namely, in the current study when d' scores from only 2-item lists were analyzed, older adults' recognition performance was impaired in the semantic interference condition compared to young adults. Additionally, older adults' recognition performance in the perceptual interference condition was not significantly different from young adults' performance. Thus, our analysis of raw d' scores found that older adults' were selectively impaired when items

were semantically related, rather than perceptually related; however, we should interpret these results from the 2-item d' analysis with caution.

The Ly et al. (2013) study failed to provide a proper manipulation of interference. Although the study's aim was to discriminate between the contributions of perceptual and semantic interference, the authors presented lures that were related to only one studied item. This paradigm fails to create a significant level of interference and, moreover, because there was no manipulation of list-length to check whether putative effects of interference were indeed due to study, inherent word properties of those single related lures could be contributing to effects. In contrast, the current study's d' (2-item) – d' (8-item) analysis directly manipulates the number of related lures and thus provides a better-controlled measurement of the effect of different types of interference.

Within the d' (2-item) – d' (8-item) analysis for both semantically and perceptually related lists, effects varied based on the item type (critical vs. related lures). This notably manifested as greater effects when examining discriminability between targets and related lures, than between targets and critical lures. We argue that the discriminability between targets and related lures is a purer and more conservative test of interference effects. First, which related words were presented during the study phase as targets and which were only presented during the test phase as related lures was randomized for each participant. This strategy should minimize any item effects. However, words that were assigned as critical lures were always the same across participants. As mentioned above, critical words have certain properties that allow the word to be a critical lure. For instance, in order to be related to all other words on a list, the word may have increased word frequency or greater initial familiarity. These inherent

word properties may be modulating the effects seen in critical lures compared to those in related lures. Accordingly, all further discussion of the findings will focus on results from the related lures analysis.

As mentioned previously, past studies have shown that older adults perform worse than young adults on the standard semantic DRM paradigm (Dennis et al., 2008; Norman & Schacter, 1997). In fact, Pidgeon & Morcom (2014) have even demonstrated that the semantic memory performance of older adults deteriorates to a greater extent than young adults with increased interference, manipulated as the degree of similarity between stimuli. However, the primary measure of false recognition in these past studies is frequently the proportion of lure false alarms. This measurement does not take into account the effects of response bias, the tendency of a participant to respond predominantly "old" or "new" (i.e., where *k* is placed between the item distributions), or the effect of age on response bias. This is an important consideration because response bias has been associated with natural aging, such that in older adults, as age increases, there is a greater tendency to make liberal responses (responding "old") during a recognition memory task (Huh, Kramer, Gazzaley, & Delis, 2006). The same effect does not exist in young adults. Therefore, previous studies that have demonstrated more false alarms for older adults may simply reflect a greater tendency to say "old" than young adults.

The current study not only addresses age group response bias differences by measuring d', but also fixes *k* between conditions. Because, in this modified DRM paradigm, semantically or perceptually related lists are intermixed, it is unlikely that a participant will know what list a word belongs to and will shift their *k* based on

perceptual or semantic relatedness. Therefore, the current results are expected to reflect true effects of age and interference type on recognition performance, rather than effects of response bias.

As argued above, we believe that the current study's analysis of d' (2-item) – d' (8-item) is able to capture the effects of semantic and perceptual interference and we believe that the representational-hierarchical account is supported by these findings. As age increases, the MTL develops structural changes that impair conjunctive representations. These conjunctive representations are not limited to conjunctions of simple features (forming whole objects), but also include associative conjunctions between semantic knowledge for objects and between objects and their context. The impaired conjunctive representations are advantageous in the semantic condition of the present modified DRM because older adults are unable to extract the associative relationships between semantically related word items that cause incorrect endorsement of related lures. In contrast, young adults with intact conjunctive representations and semantic associative extraction would suffer from interference as in the standard DRM paradigm.

We also expected that perceptually similar words would have worse discriminability between related lures and targets for older adults than young adults. This recognition memory impairment was predicted to occur because older adults with impaired conjunction representations would be unable to resolve simple-feature interference. Even though the results reflected a trend in the direction of this prediction, we did not see a significant effect, perhaps because the study failed to create sufficient simple-feature interference, thus allowing better older adult performance than expected.

Additionally, the small sample size could have impacted the power for detecting this effect. However, the fact that the perceptual and semantic interference had opposing effects on older versus younger adults' memory was instructive: perceptual interference tended to impair older participants while not affecting younger participants, whereas semantic interference tended to impair younger participants while not affecting older participants. This finding is in line with the predictions of the representational-hierarchical account, and suggests that age-related changes in conjunctive representations may account for age-related changes in memory.

CHAPTER 4

GENERAL DISCUSSION

4.1 Overview of Findings and Future Directions

The two studies included here set out to explore a main feature of the representational-hierarchical theory: the effects of interference on neural signatures of familiarity and on recognition memory performance. Experiment 1 was inconclusive in testing the prediction that posterior ventral visual stream representations of novel objects would bear neural signatures of familiarity after perceptual interference in healthy participants. We believe this does not necessarily refute the prediction of the representational-hierarchical theory, but reflects the limitations of the current experimental design and highlights possible difficulties in exploring neural representations within the brain. We encourage future work testing this prediction to utilize more controlled stimuli and to take advantage of both univariate and multivariate analyses.

Experiment 2 did support the prediction that older adults experience memory impairments from feature-level interference, but are paradoxically shielded from semantic-level interference. These findings support the representational-hierarchical account and suggest that this theory may have explanatory power for how age-related changes to the medial temporal lobe can affect memory. Future work should examine the effect of simple-level interference in aging further and include studies on populations with more extensive changes in conjunctive representations (e.g., Alzheimer's disease, Mild Cognitive Impairment).

In addition to providing evidence for the representational-hierarchical account, Experiment 2 also builds upon the pre-existing DRM literature. Firstly, the study contributes to the body of evidence that supports specific, content-dependent memory deficits for older adults, rather than global recognition memory impairments. Secondly, our findings highlight the importance of controlling for item effects and incorporating response bias while examining effects within the DRM paradigm. Future studies examining DRM memory impairments should incorporate these more rigorous methodologies.

Table 1: Older Adult Average Raw Scores for Neuropsychological Battery

Test (Maximum score)	M (SD)
MMSE (/30)	29.0 (1.1)
WMS-IV LM Immediate Recall (/50)	23.3 (5.4)
WMS-IV LM Delayed Recall (/50, 20-min delay)	19.3 (6.5)
WMS-IV LM Recognition (/30)	22.2 (3.9)
Trails A	24.7 s (7.3 s)
Trails B	65.1 s (35.9 s)
WAIS-IV Digit Span Forward (/9)	6.6 (1.1)
WAIS-IV Digit Span Backward (/8)	4.7 (1.2)
VOSP Silhouettes (/30)	19.6 (4.8)

Note: The mean (M) performance on all cognitive tasks was within the normal range relative to established norms or within established passing cutoff scores. MMSE = Mini-Mental State Examination; WMS-IV LM = Wechsler Memory Scale, 4th ed., Logical Memory subtest; WAIS-IV = Wechsler Adult Intelligence Scale, 4th ed.; VOSP = Visual Object Space Perception battery.

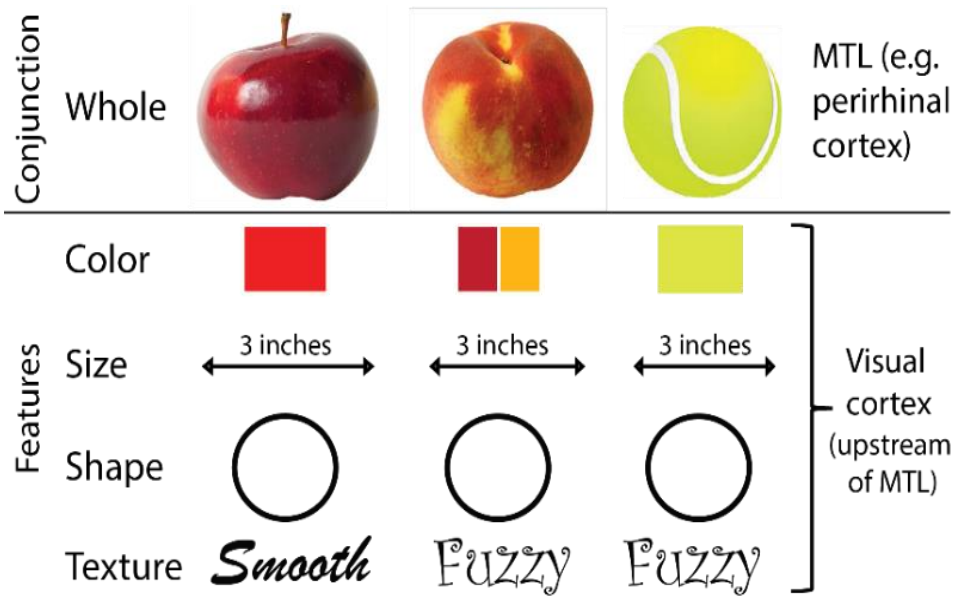


Figure 1: Illustration of Shared Posterior Simple Features and Unique Anterior Conjunctions of Features.

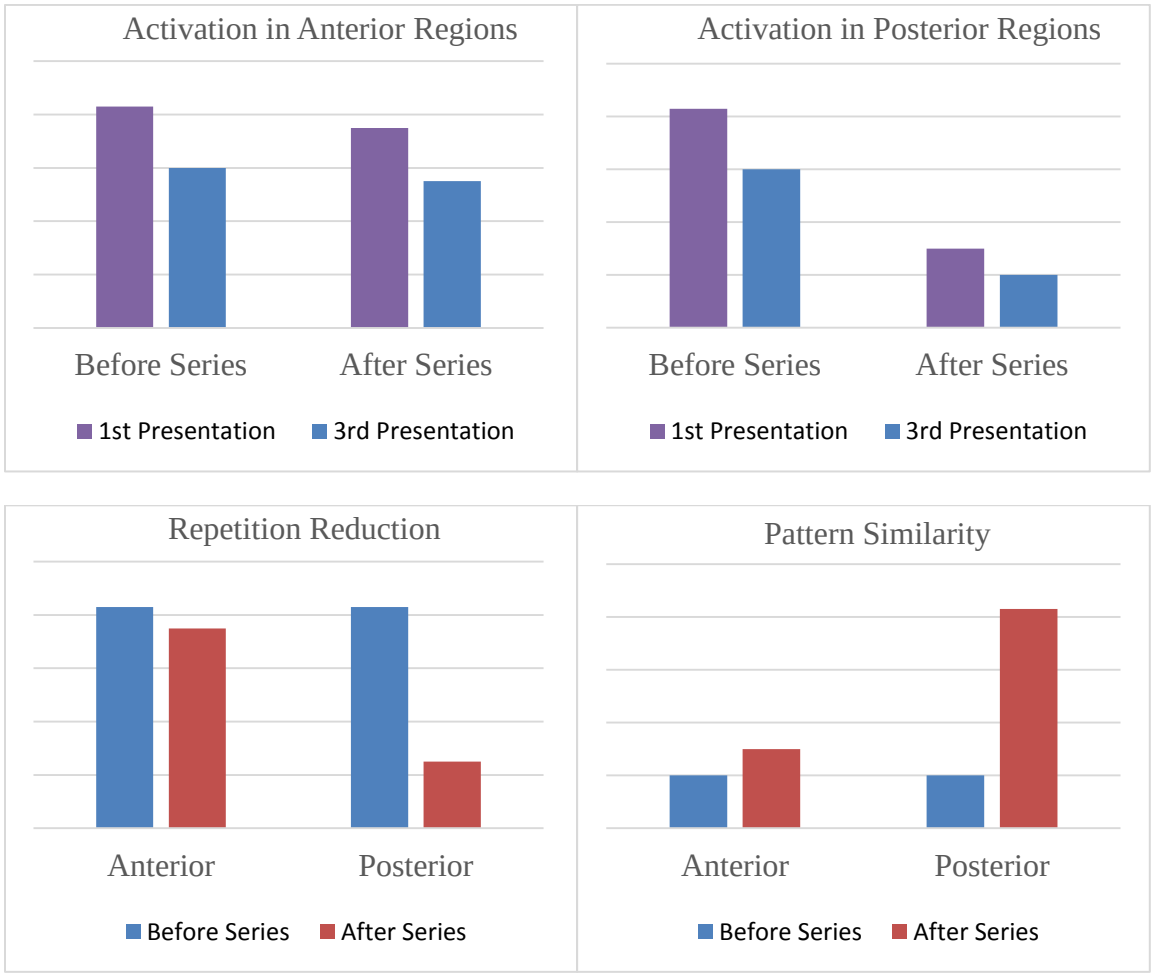


Figure 2: Predicted Changes in Repetition Reduction (RR) and Pattern Similarity (PS) after a Long Series of Same-Category Images in High Interference Runs. The top row is an example of possible neural activation from the first presentation to the third presentation of a unique object. The bottom row demonstrates how this example would be represented as RR, i.e., the subtraction of the third from the first presentation (a decrease in RR in posterior areas after the series) and as PS, i.e., the correlation between third and first presentations (an increase in PS in posterior areas after the series).

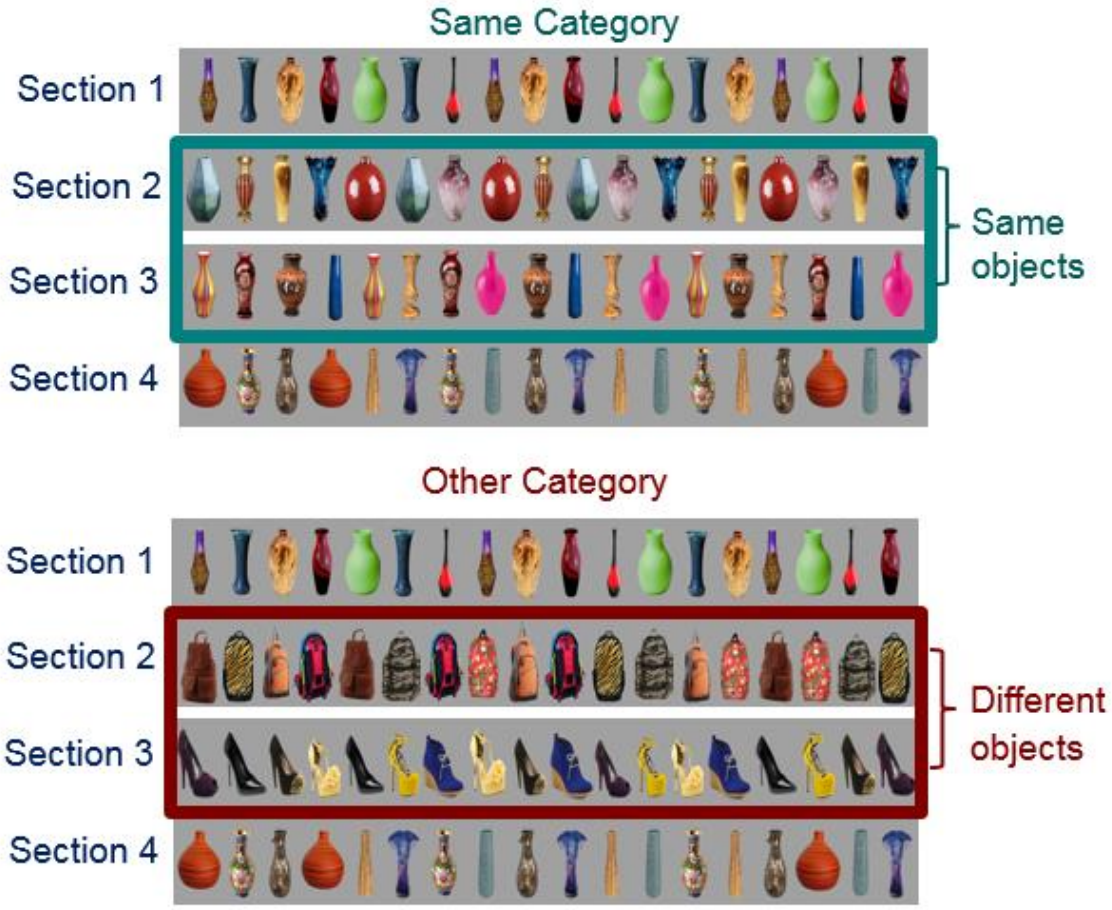


Figure 3: Examples of a Same Category (High Interference) and an Other Category (Low Interference) Run.

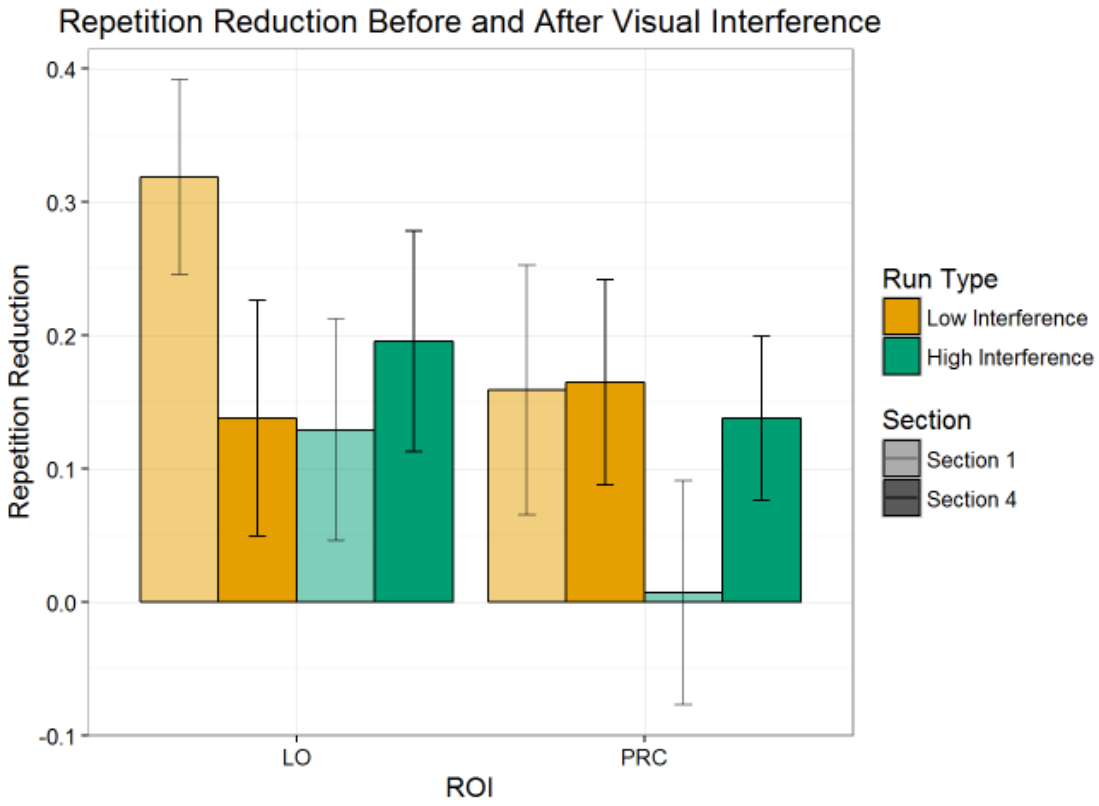


Figure 4: Effects of ROI, Section, and Interference on Repetition Reduction (RR). Error bars are standard error of the mean.

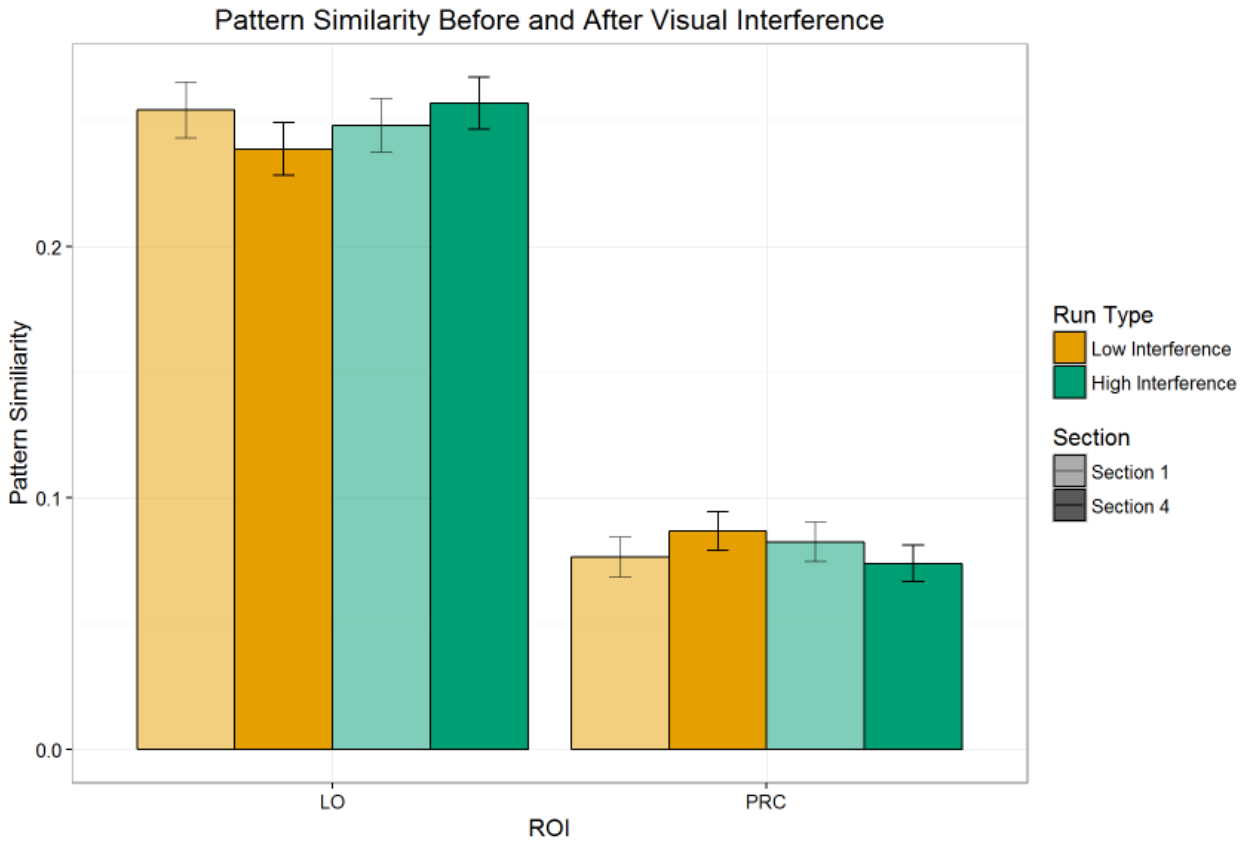


Figure 5: Effects of ROI, Section, and Interference on Pattern Similarity (PS). Error bars are standard error of the mean.

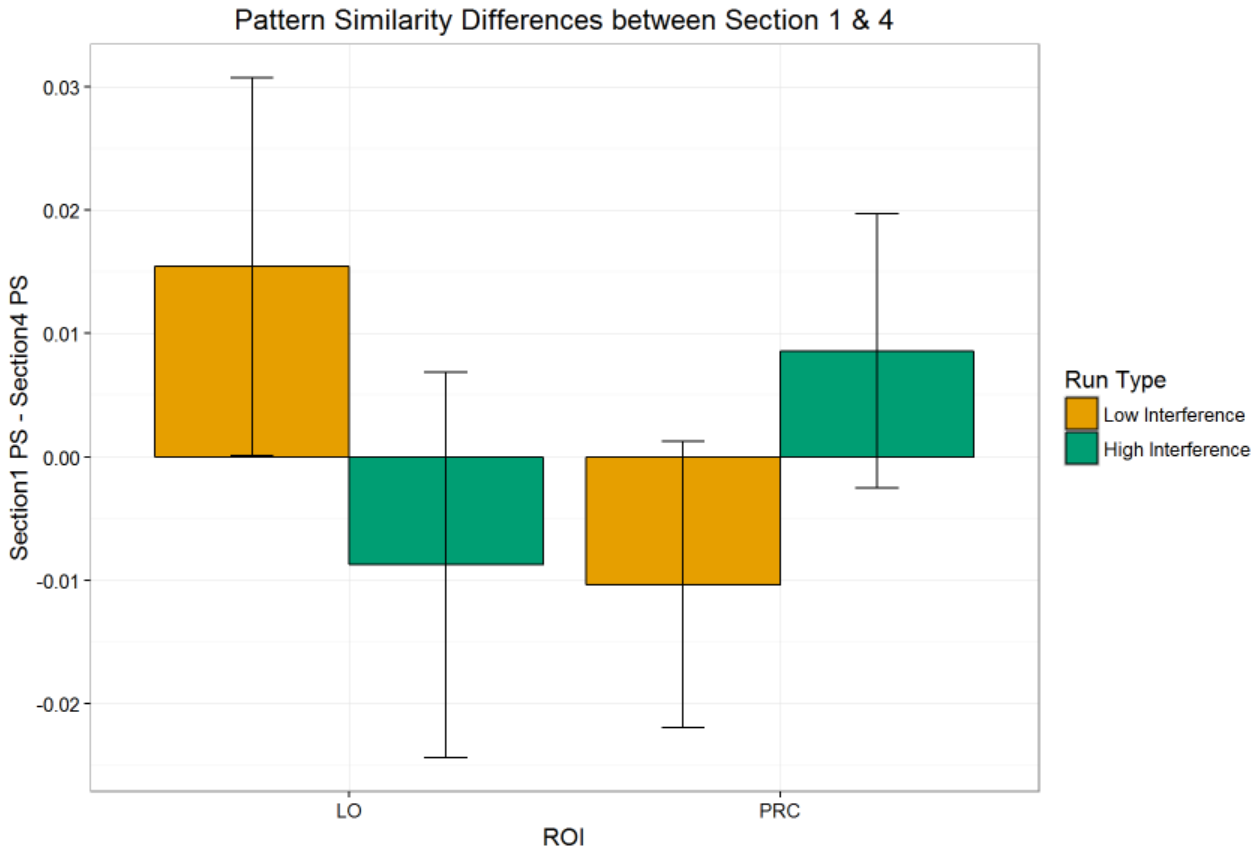


Figure 6: Effects of ROI and Interference on Pattern Similarity (PS) Difference between Section 1 and 4. Error bars are standard error of the mean.

	Perceptually Similar Lists	Semantically Similar Lists
Type of interference leading to false alarms	Simple perceptual features	Conceptual/object semantic knowledge (through association)
Readiness of interference	Available at stimulus presentation	Must be constructed/extracted at time of encoding
Effect of impaired conjunction representations in MTL	Cannot resolve simple-feature interference	Cannot extract semantic interference
Predicted DRM performance for older participants (relative to young controls)	Higher false alarms for novel perceptually similar prototypes	Lower false alarms for novel semantically similar prototypes

Figure 7: Predicted DRM Performance for Older Adults.

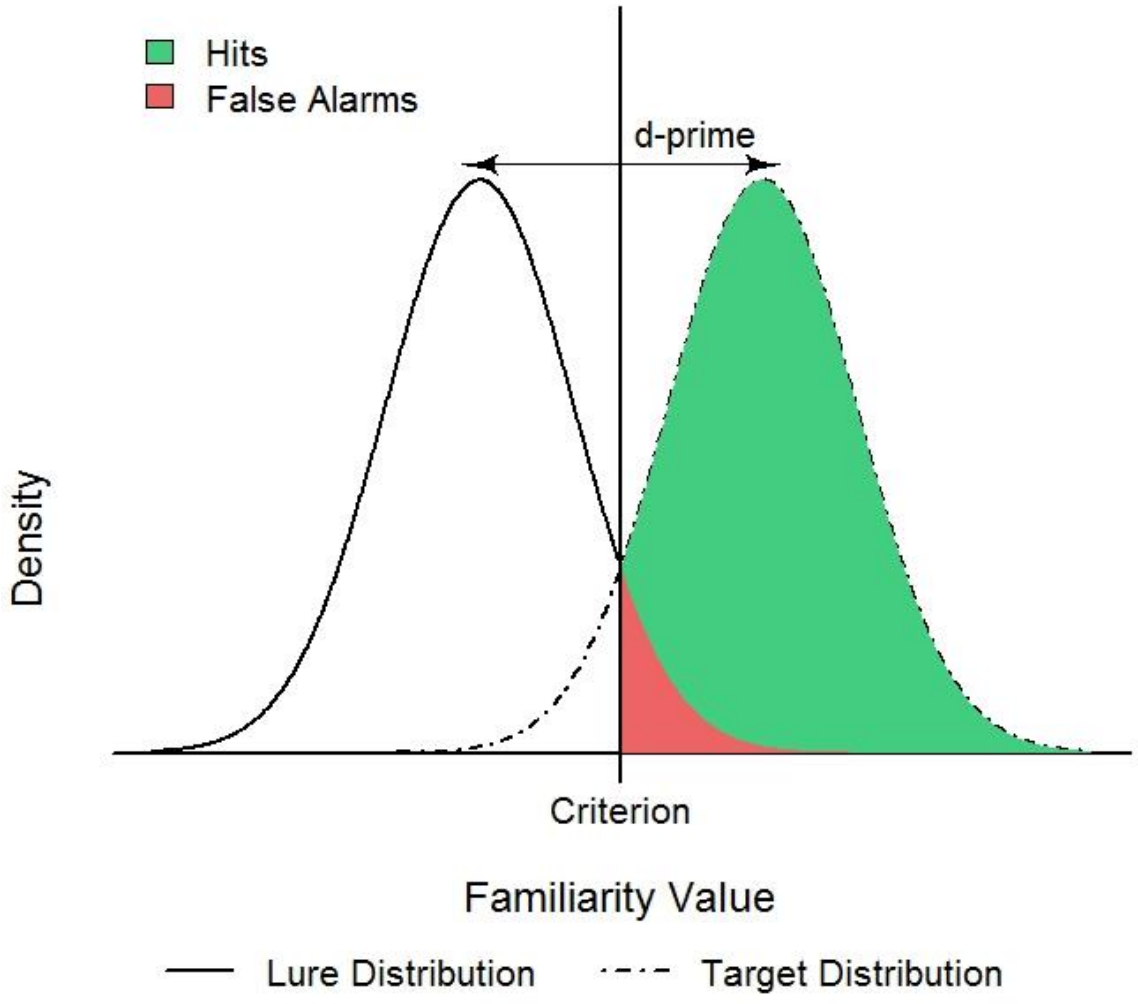


Figure 8: Illustration of Signal Detection Theory Measurements.

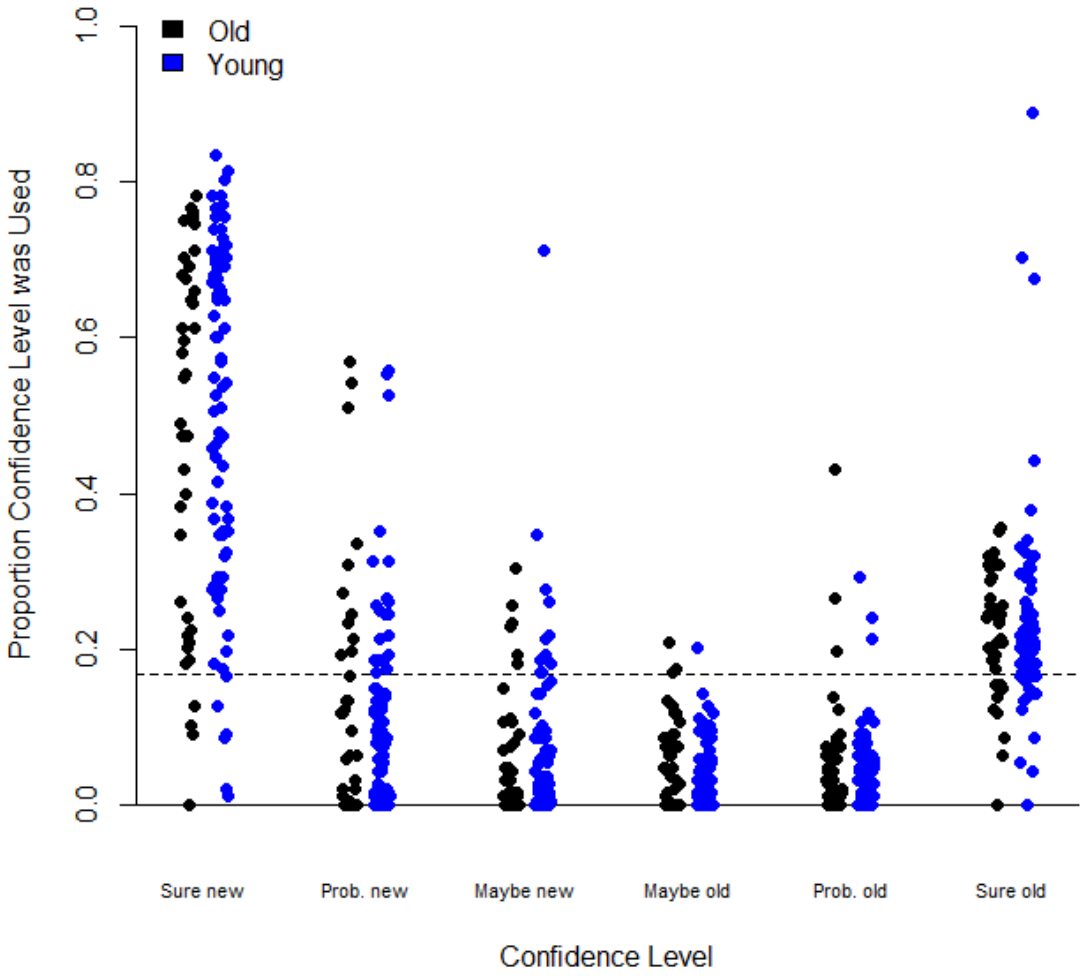


Figure 9: Proportion of Times a Confidence Level was used by Older and Young Subjects. Each point shows the proportion of responses for one subject averaged across conditions. The dotted line shows proportions corresponding to equal use of each level.

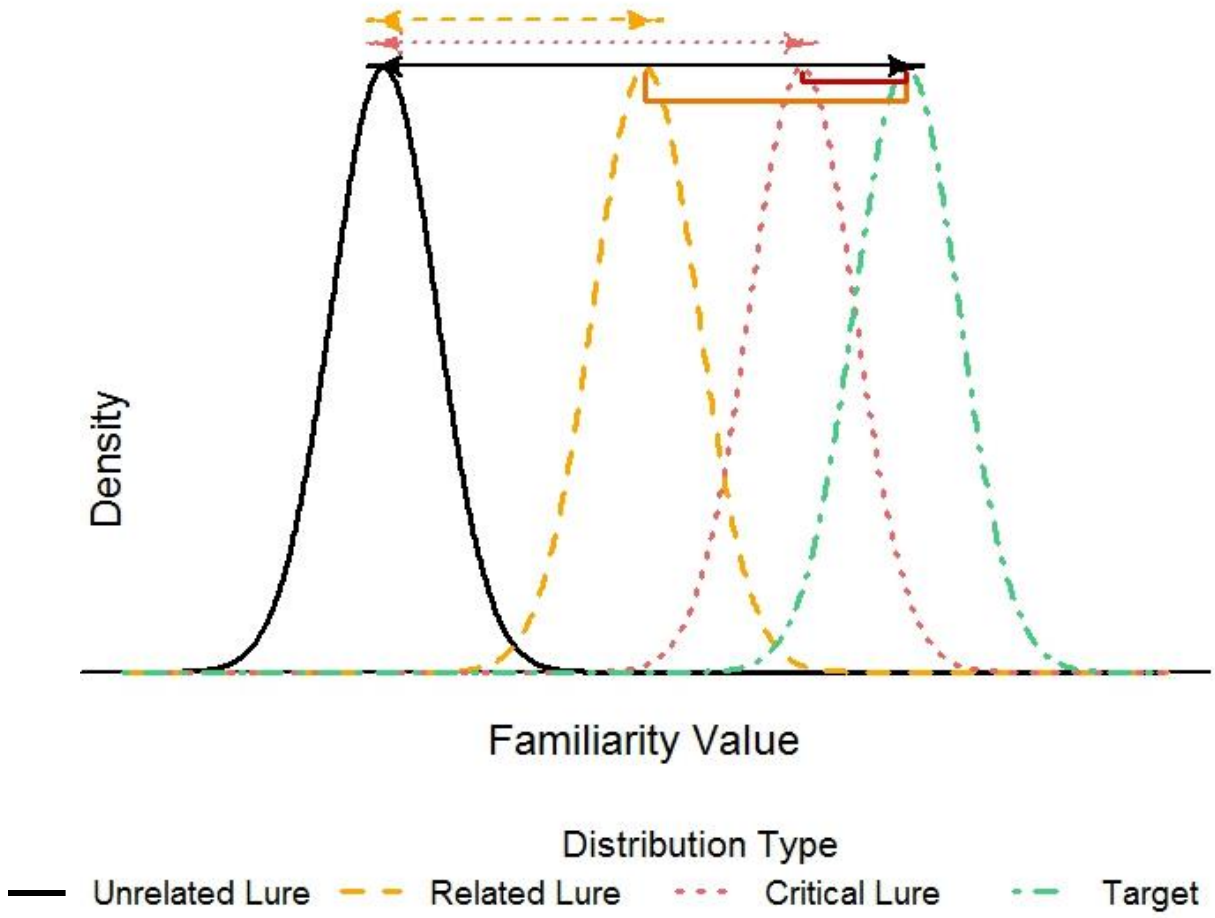


Figure 10: Illustration of the Process to Obtain d' Values of Interest for a Condition. Each arrow represents a d' value: discriminability between unrelated lures and targets (black); discriminability between unrelated lures and critical lures (red); and discriminability between unrelated lures and related lures (orange). To obtain d' values of interest (i.e., discriminability between targets and critical lures and discriminability between targets and related lures, represented by the darker orange and red brackets, respectively) the d' of unrelated lures and critical lures (red arrow) and d' of unrelated lures and related lures (orange arrow) are subtracted from the d' of unrelated lures and targets (black arrow).

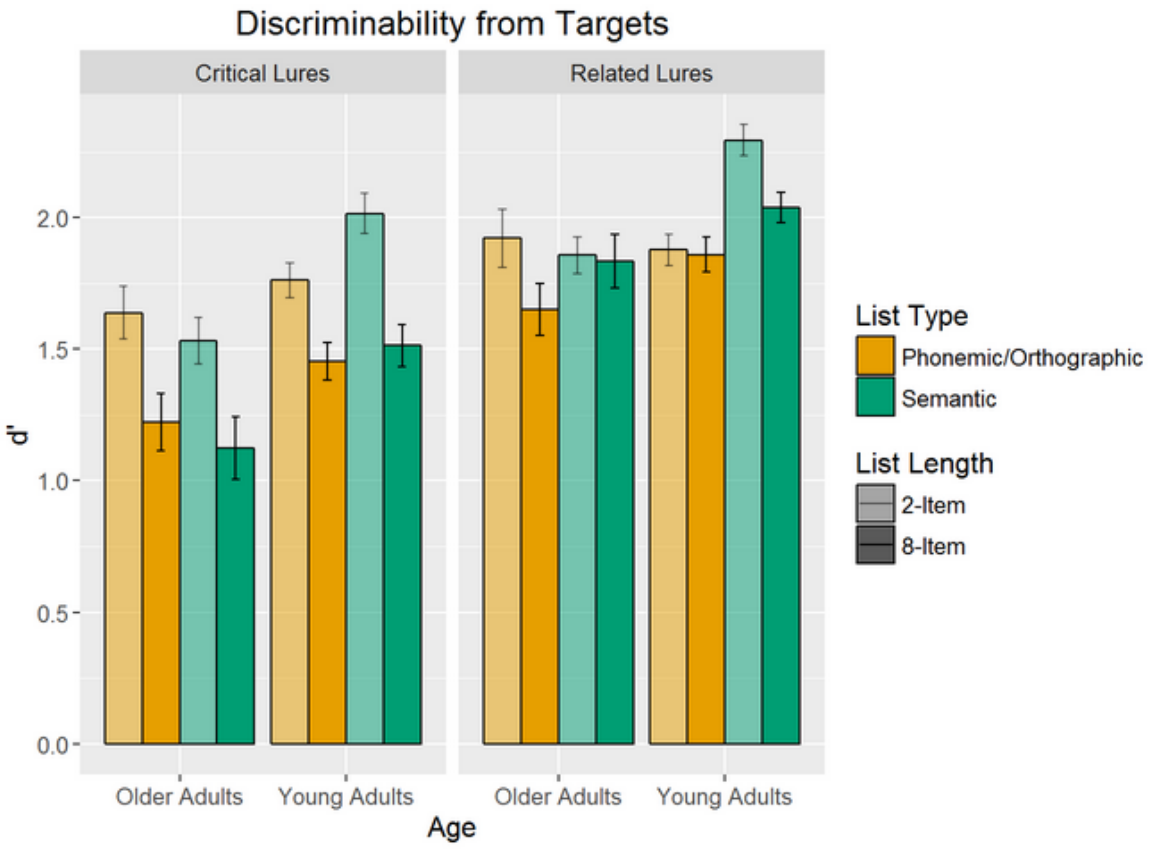


Figure 11: Effects of List Length, List Type, Item Type, and Age Group on Discriminability from Targets. Error bars are standard error of the mean.

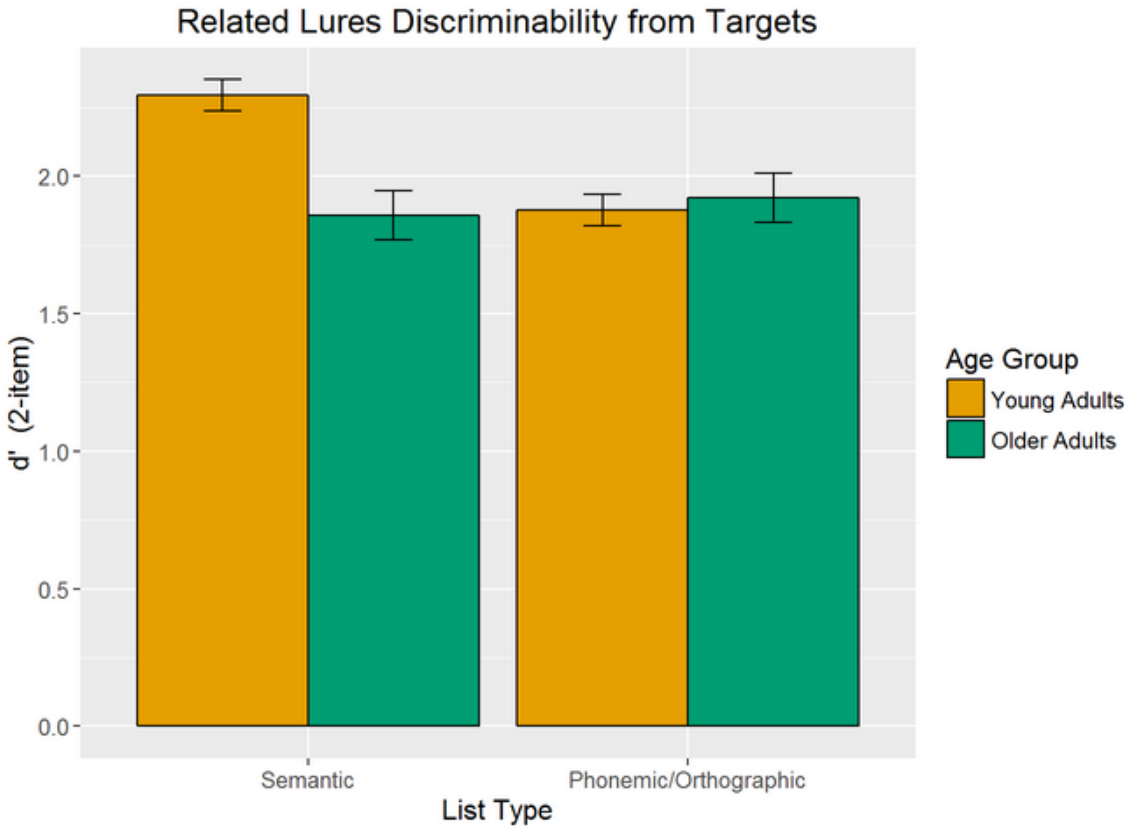


Figure 12: Comparison of Ly et al.'s (2013) List Type and Age Group Effects on Related Lure Discriminability from Targets. Error bars are standard error of the mean.

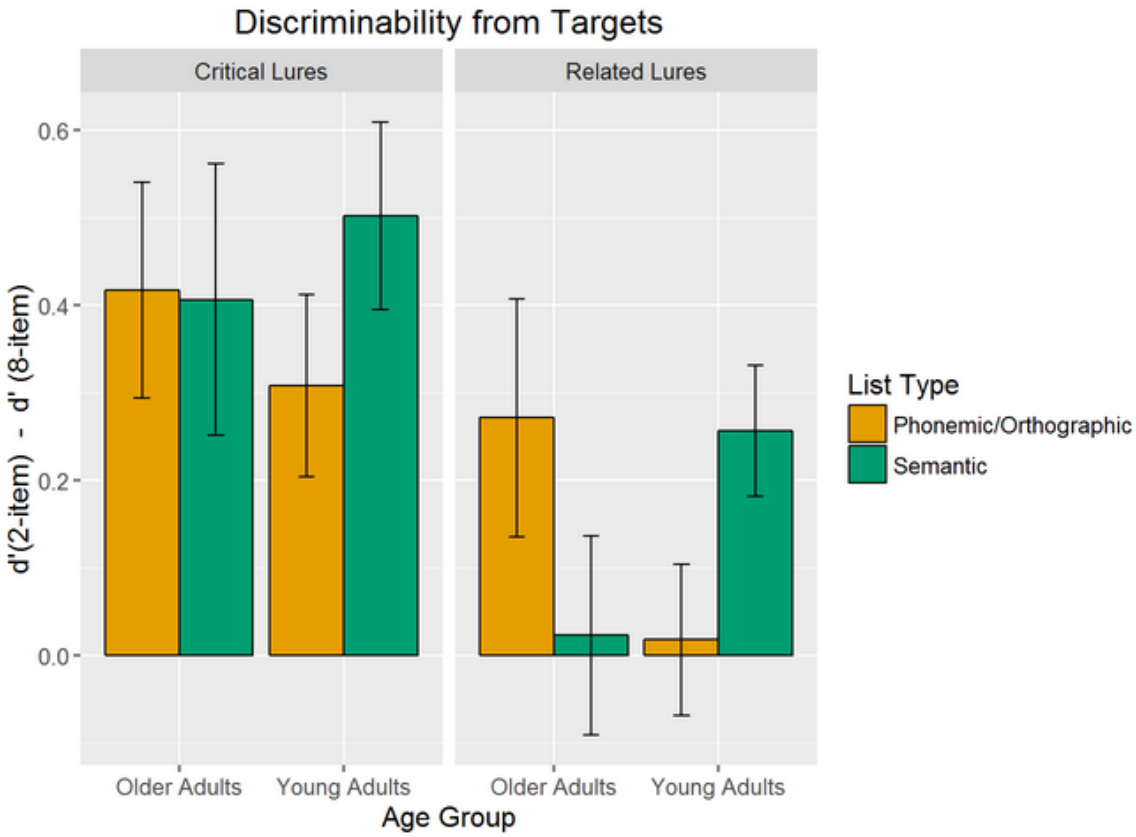


Figure 13: Effects of List Type, Item Type, and Age Group on Study-Related Interference for Discriminability from Targets. Error bars are standard error of the mean.

APPENDIX A

EXPERIMENT 2 SEMANTIC WORD LISTS

Astronaut	**Butterfly**	**Castle**	**Comedian**	**Diamond**
Atmosphere	Camouflage	Chateau	Buffon	Brilliance
Cosmonaut	Caterpillar	Courtyard	Clown	Carat
Gravity	Cocoon	Dungeon	Comic	Emerald
Orbiting	Dragonfly	Feudal	Humorist	Glittering
Rocket	Flutter	Fortress	Improvisation	Hardness
Satellite	Fragile	Mansion	Joker	Precious
Shuttle	Metamorphosis	Medieval	Lampoon	Priceless
Spaceman	Monarch	Stronghold	Monologue	Rhinestones
Voyager	Slight	Throne	Punster	Rubies
Weightlessness	Wings	Towers	Slapstick	Sparkle

Dinosaur	**Fitness**	**Gambler**	**Infant**	**Lunatic**
Amphibians	Aerobics	Bettor	Babble	Asylum
Artifacts	Barbells	Blackjack	Cradle	Demented
Brontosaurus	Biceps	Bookie	Diapers	Deranged
Extinction	Exertion	Casino	Highchair	Hallucinations
Fossils	Jogging	Jackpot	Lullaby	Insanity
Glaciers	Nutrition	Lottery	Pacifier	Madman
Mammoth	Physique	Poker	Rattle	Manic
Reptiles	Sweating	Roulette	Stork	Psychopath
Skeletons	Toning	Stakes	Stroller	Psychotic
Swamps	Workout	Wager	Teething	Ranting

Magician	**Phantom**	**Pyramid**	**Robbery**	**Tornado**
Conjure	Apparition	Catacombs	Bandit	Cyclone
Enchanted	Beckon	Egyptian	Booty	Funnel
Hypnotist	Ghost	Embalming	Burglary	Gusts
Juggling	Ghoul	Hieroglyphics	Holdup	Sirens
Rabbit	Goblins	Mummies	Mugging	Spiral
Sorcerer	Haunting	Pharaoh	Stealing	Twister
Trickster	Paranormal	Tombs	Stickup	Typhoon
Vanish	Specter	Triangular	Theft	Whirling
Wizard	Spooky	Underworld	Wallet	Whirlwind

APPENDIX B

EXPERIMENT 2 PHONEMIC/ORTHOGRAPHIC WORD LISTS

Boon	**Bun**	**Cat**	**Cop**	**Fate**
Boom	Bud	Bat	Bop	Date
Boos	Bum	Cab	Cob	Face
Boot	Bus	Cam	Cod	Fade
Coon	But	Cap	Cog	Fake
Goon	Fun	Fat	Con	Fame
Loon	Gun	Hat	Cot	Gate
Moon	Nun	Mat	Hop	Hate
Noon	Pun	Pat	Mop	Late
Soon	Run	Rat	Pop	Mate
Toon	Sun	Sat	Top	Rate

Mire	**Role**	**Sip**	**Teal**	**West**
Dire	Dole	Dip	Deal	Best
Fire	Hole	Hip	Heal	Lest
Hire	Mole	Lip	Meal	Nest
Mice	Pole	Nip	Peal	Pest
Mike	Robe	Rip	Real	Rest
Mile	Rode	Sin	Seal	Test
Mime	Rope	Sis	Team	Vest
Mine	Rose	Sit	Teas	Welt
Tire	Rote	Six	Teat	Went
Wire	Sole	Tip	Veal	Wept

APPENDIX C

EXPERIMENT 2 EXTRA WORDS

Semantic		**Phonemic/Orthographic**
Antiquity	Opossum	Bird
Apartment	Pauper	Book
Attic	Piccolo	Bout
Bagel	Podium	Bur
Biologist	Promenade	Coin
Bison	Purple	Cow
Canvas	Sable	Foil
Carport	Schoolyard	Fur
Convenience	Scissors	Joy
Gazette	Silhouette	Lawn
Gutter	Stationer	Loud
Honeycomb	Storeroom	Now
Housecoat	Synopsis	Null
Industry	Thesaurus	Perk
Inferno	Thicket	Pull
Invitation	Tortilla	Raw
Jargon	Tribesman	Saw
Jasmine	Triplicate	Toy
Linguistics	Undergrowth	Wood
Mechanical	Unformed	Yaw
Monoxide	Warmhearted	
Mooring		

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