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Value-Directed Remembering and Aging: Examination of Supporting Mechanisms and Effects on Memory Quality

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Value-Directed Remembering and Aging: Examination of

Supporting Mechanisms and Effects on Memory Quality

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Psychology

by

Joseph Peter Hennessee

2018

ABSTRACT OF THE DISSERTATION

Value-Directed Remembering and Aging: Examination of

Supporting Mechanisms and Effects on Memory Quality

by

Joseph Peter Hennessee

Doctor of Philosophy in Psychology

University of California, Los Angeles, 2018

Professor Barbara Knowlton, Chair

Aging is associated with declines in memory performance and profound functional and structural changes in the brain, though older adult's ability to selectively learn and retrieve valuable information appears to be well preserved. Prior research suggests that older adults differentially employ elaborative encoding strategies when encoding valuable items and selectively allocate attention to these items, as reviewed in Chapter 1. The underlying aims of the current study were to examine how this selective learning affects different aspects of memory and what cognitive and neural mechanisms may support older adult's effective learning of valuable information.

Chapter 2 describes findings from a project aimed at determining how value-directed remembering affects different aspects of memory. This research suggests that selectively encoding valuable items is associated with greater recognition performance, higher confidence, and increased recollection in both younger and older adults. Although age-related declines in

recollection are typically observed, value's enhancement of item recollection appears to be intact in healthy aging. Selectively encoding valuable items also resulted in stronger binding between items and incidentally learned task-relevant details, perhaps at the expense of encoding extraneous details. Older adults did not demonstrate greater item-location memory for valuable items, suggesting that value's influence on associative binding may be diminished in aging.

Chapters 3 and 4 describe two projects designed to investigate how strategic and automatic processes contribute to value-directed remembering, and whether differences in the structural integrity of white matter tracts predicts differences in older adult's ability to selectively learn based on value. The findings of these two studies suggest that younger adults are relying on a more automatic reward circuit involving the nucleus accumbens and ventral tegmental area, whereas older adults rely on semantic processing in the inferior fronto-occipital fasciculus (IFOF). Older adults may be relying on the IFOF in a compensatory manner. The implications of these findings for theories of aging and learning are discussed in Chapter 5.

The dissertation of Joseph Peter Hennessee is approved.

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Chapter 2 is a reprint of a 2018 publication in Psychology and Aging. Copyright © 2018 American Psychological Association. Reproduced with permission. The official citation that should be used in referencing this material is Hennessee, J. P., Knowlton, B. J., & Castel, A. D. (2018). The effects of value on context-item associative memory in younger and older adults. *Psychology and Aging, 33*(1), 46-56. https://dx.doi.org/10.1037/pag0000202. This article may not exactly replicate the authoritative document published in the APA journal. It is not the copy of record. No further reproduction or distribution is permitted without written permission from the American Psychological Association. The dissertation author was the primary author of this article and Professor Alan Castel was the principal investigator. Professor Barbara Knowlton helped considerably with designing the experiments, interpreting results, and manuscript editing.

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INVITED PRESENTATIONS

Hennessee, J. P. (Presenter), Knowlton, B. J., & Castel, A. D. (2017). *Value-Based Recognition and Executive Functioning in Aging.* Presented at the 14th Bay Area Memory Meeting, San Francisco, CA.

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Hennessee, J. P. (2015). *Value Selectively Enhances Recollection.* Presented at the Graduate Student Datablitz, University of California Irvine, CA.

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Hennessee, J. P. (Presenter), Saetern, N. F., Rezai, J., Ha, A., & Johnson, C. S. (2012). *The Relationship Between Perceiver and Source Characteristics With the Perceived Intentions Behind Directed Social Comparisons.* Presented at the 55th Spartan Psychological Association Research Conference, San José, CA.

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Saetern, N. F., Rezai, J., Hennessee, J. P., Ha, A., & Johnson, C. S. (2012). *The Use of Directed Comparisons To Meet Goals.* Poster presented at the 55th Spartan Psychological Association Research Conference, San José, CA.

Chapter 1

General Introduction

1.1 Value-Directed Remembering and Aging

In everyday life, much of learning is goal-driven; people want to learn information that will be valuable to them in the future. Because it is often impossible to perfectly learn and retrieve all information one observes, optimal learning typically requires the selection of more important information over less important information. To examine how value shapes learning, Castel, Benjamin, Craik, & Watkins (2002) established the value-directed remembering (VDR) design, wherein participants learn words associated with point-values and earn those points for correct recall. These point-values are used to simulate that some information is more important than other information, and participants are instructed that their goal is to earn a high score. A wide literature supports that items paired with high point-values or high monetary-values at encoding are more likely to be later retrieved (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Ariel, Price, & Hertzog, 2015; Castel, Murayama, Friedman, McGillivray, & Link, 2013). In many of these studies, participants experience the limitations of their ability to freely recall items through feedback on successive tests. Participants thus learn to differentially encode high-value items to maximize their performance. This selective encoding of valuable information requires attentional control, goal maintenance, and inhibition of less important information (Balota & Faust, 2001; Waszak, Li, & Hommel, 2010; Zelazo, Craik, & Booth, 2004).

Even relatively healthy aging is associated with substantial declines in free recall and recognition memory (Cohen, Rissman, Suthana, Castel, & Knowlton, 2016; Spaniol, Schain, & Bowen, 2013), but older adults are often as good at college students at remembering the most

valuable items (Castel et al., 2002; Castel et al., 2011). This research illustrates that older adults often adapt to their limitations in memory by selectively focusing on what information is most valuable to them. Much of the research on VDR in aging uses free recall testing, but some research suggests that VDR is also present on recognition tasks (Hennessee, Castel, & Knowlton, 2017; Spaniol, Schain, & Bowen, 2013). In Spaniol, Schain, and Bowen (2013), older and younger adults studied a large selection of scenic images that were paired with either a high ($1) or low ($0.01) value cue depicting how much they would earn for later recognition. Compared with younger adults, older adults displayed a worse ability to distinguish old items from new ones due to a higher false alarm rate. High-value items were more likely to be recognized at test, and although older adults exhibited impaired picture memory relative to younger adults, they benefitted from value to a similar extent. It was noteworthy that strong value effects were observed despite their use of recognition testing. The number of individual items that can be free recalled is typically much more limited than the amount of items that can be recognized (Standing, 1973), thus one should not need to selectively ignore low-value items to the same extent on a recognition test. Spaniol, Schain, and Bowen's (2013) finding that VDR occurs on a recognition test highlights how robust of an effect value has on encoding. An added benefit of testing VDR with a recognition test is that the participants' ability to use retrieval strategies—such as reporting valuable items first—is limited relative to free recall, thus this finding provides additional support that VDR is due to differences in encoding.

The ability to selectively encode information based on value is important for efficient learning and the above research suggests that this ability is intact in older adults (Castel et al., 2002; Castel et al., 2011; Spaniol, Schain, & Bowen, 2013). However, the mechanisms behind VDR and the effects of selectively encoding valuable items are still unclear. For example, are

older adults better at retrieving high-value items because they bind those items with associated details to form rich episodic memories, or do they selectively focus on the item itself at the expense of encoding episodic details? Is VDR primarily due to selectively attending to valuable stimuli, encoding valuable stimuli in deeper more elaborative ways, or contributions of a more automatic mechanism? Are there neurological differences, such as differences in the integrity of white matter tracts, that explain why some older adults show larger effects of value on memory than others? These three questions regarding VDR and aging are the basis for this dissertational work and will be described more thoroughly below.

1.2 Recollection, Familiarity, and Associative Memory in Aging

Every day, people must be able to recall both simple facts, such as whether one has paid a bill on time, and episodic content, such as recounting details about a vacation to a curious friend. This ability to recall both semantic and episodic information efficiently is an important part of healthy cognitive aging. However, a considerable body of research suggests that while semantic memory is largely spared in aging, retrieving episodic details becomes much more difficult (Koen & Yonelinas, 2014; Piolino et al., 2010).

Before addressing why episodic memory is impaired in aging, first I will describe what episodic memory is and how it is measured. Episodic memory describes our ability not just to retrieve a single item from memory, but being able to relive the experience in mind. This typically involves recollecting thoughts or feelings associated with the item or its context at retrieval (Tulving, 1985). To assess episodic memory, Tulving (1985) established a distinction between *remembering* and *knowing* in the experience of recognition. Remembering is the conscious recollection of a previous experience or event, typically including memory for details related with the episode. Knowing instead involves confidently recognizing something without

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consciously recollecting the original experience or related details. This is often described as a feeling of familiarity without conscious memory of the learning experience. In the dual-process model remembering and knowing are thought to reflect separate recollection and familiarity memory processes, respectively (Yonelinas, 1999). These two types of memory may be assessed via self-report after providing the participant with detailed instructions as to what constitutes *remembering* the learning experience and related episodic details versus simply *knowing* that the item was viewed before. Research contrasting Remember-Know judgments with recognition confidence suggest that these constructs do not just reflect a continuum of confidence (Gardiner & Java, 1990; Geraci, McCabe, & Guillory, 2009), particularly when instructions are well-designed.

Self-report data are particularly useful when we are interested in the conscious experience of retrieval and the subjective quality of a memory, but this methodology comes with the caveats that participants may fail to understand the distinction between remembering and knowing and sometimes they produce false recollection responses to new items. Older adults are particularly prone to having false feelings of recollection for new items, likely due to impairment in monitoring their retrieval (Dennis, Bowman, & Preston, 2014; Duarte, Graham, & Henson, 2010; Pitarque, Sales, Meléndez, & Algarabel, 2015). Alternatively, episodic memory can be assessed by asking participants if they can recollect details present during learning, such as the spatial location of the item (e.g., left or right) or the sex of someone aurally presenting the items, as is commonly done in source memory tasks. This provides a more quantifiable and perhaps objective measure of recollection, but it comes with its own issues. First, source details are sometimes retrievable when the item is only familiar (Hicks, Marsh, & Ritschel, 2002), suggesting that correct source memory judgments are not always accompanied by recollection of

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the learning experience. One interpretation of this finding is that participants may sometimes develop weaker non-declarative memory of source details, and though they are unable to consciously retrieve the detail, their guesses are better than chance. Second, one can recollect thoughts associated with the item at test or source details that the experimenter does not ask about, so an incorrect source response does not constitute an absence of recollection. Therefore, both studies that assess Remember-Know judgments and memory for associated details, such as source memory, provide uniquely important information about the recollection experience and come with their own strengths and weaknesses.

Koen and Yonelinas (2014) performed a meta-analysis of 25 healthy aging studies to determine how much recollection and familiarity change in aging. These studies measured recollection and familiarity using Remember-Know judgements, source memory, or a receiver operating characteristic (ROC) analysis, and the meta-analysis found that healthy aging was related with a substantial decline in recollection (d_w = -0.75) and a more modest, yet significant, decrease in familiarity (d_w = -0.27). The Remember-Know findings of Clarys, Isingrini, and Gana (2002) followed this pattern nicely, as they found older adults gave fewer Remember responses at test, but had no reduction in Know responses. A potential interpretation is that older adults simply use the Remember response more conservatively, and do not actually have substantial differences in recollection. However, neuroimaging and EEG studies show that in older adults there is typically marked decline in the volume and activation of recollection-based regions, such as the hippocampus and prefrontal cortex, and event related potential waveforms for recollection, but not familiarity, are substantially impaired in aging (Friedman, 2013; Gunning-Dixon, Brickman, Cheng, & Alexopoulos, 2009; McDonough, Cervantes, Gray, &

Gallo, 2014; McDonough, Wong, & Gallo, 2013). Thus, the above results demonstrate that aging is associated with actual deficits in recollection and not merely differences in responding.

Anderson et al. (2008) provides a great example of how source memory performance typically changes in aging; they observed that healthy older adults displayed nearly equivalent item memory as younger adults, but their memory for whether the item was presented visually or aurally was substantially impaired. Recollection of episodic details (presentation), but not item familiarity was impaired in older adults. They likewise found that frontal lobe functioning, which they estimated using a neuropsychological test, was inversely related with recollection in healthy older adults. The prefrontal cortex has been implicated in the recollection of context-dependent memories via its role in attentional control, and the search and monitoring of contextual information (see Skinner & Fernandez, 2007), thus impairment to these processes may explain older adults' difficulty in retrieving source details. Taken together, the above research suggests that although familiarity is largely spared in healthy aging, recollection and memory for associated details declines. Chapter 2 of this dissertation addresses how selectively learning valuable items affects younger and older adults' experiences of recollection and memory for associated details.

1.3 Mechanisms Supporting Value-Directed Remembering

Although there is much support for VDR, it is still unknown whether strategic or relatively automatic processes contribute more to this effect. Selective-attention is thought to play an important role in VDR, such that attentional resources are allocated to learning more valuable information. When given a limited time to study items, participants disproportionately allocate that time to studying the most valuable items (Ariel, Dunlosky, & Bailey, 2009; Ariel, Price, & Hertzog, 2015; Castel et al., 2013), and this increased study time is associated with

superior memory for those items (Castel et al., 2013). This suggests that much of the selective attention allocation in VDR is intentional. Although high-value items receive increased attention, a commonly used and often effective learning strategy is to ignore low-value items (Ariel, Price, & Hertzog, 2015; Robison & Unsworth, 2017). Considering that one can only remember a limited number of items for a recall test, selectively encoding valuable items—by ignoring low-value ones—is a prudent strategy. It is also well documented that value cues are particularly effective at capturing attention (Anderson, 2013; Hickey, Chelazzi, & Theeuwes, 2010; Kiss, Driver, & Eimer, 2009). High-value cues promote pupil dilation—a measure indicative of increased attention—suggesting that learners selectively allocate attention to valuable items (Ariel & Castel, 2014).

Elaborative encoding also likely plays a role in VDR as learners change their encoding strategy to more deeply and effectively learn valuable items. For example, in Ariel, Price, & Hertzog (2015), both older and younger adults used more effective learning strategies for learning high-value word pairs, including generating an image or word that mediated the relationship between the word pair, putting the word pair into a sentence, or thinking about how the words were semantically related. When participants used these more elaborative encoding strategies, as opposed to rote memorization, they had substantially better retrieval. This is likely because these strategies produce deeper semantic processing that enhances encoding (Craik & Lockhart, 1972; Richardson, 1998). This adaptive alteration of encoding strategy based on item-value has also been observed in more recent research in younger adults (Cohen, Rissman, Hoyhannisyan, Castel, & Knowlton, 2017). Research suggests that elaborative encoding strategies improve memory by increasing recollection of the item at retrieval, but with little change to item familiarity (Fawcett, Lawrence, & Taylor, 2016; Gardiner, Gawlik, &

Richardson-Klavehn, 1994). Familiarity is instead influenced by the amount of maintenance rehearsal. Thus, elaborative encoding may be a primary reason why valuable items are more likely to be recollected at test in younger adults (Hennessee, Castel, & Knowlton, 2017). As older adults typically show deficits in episodic memory (Koen & Yonelinas, 2014), it is uncertain if they would exhibit this same increase in recollection when selectively learning valuable information.

Although the above research suggests that participants are strategically allocating attention and selecting their encoding strategy based on item-value, a wide range of research also suggests that VDR may occur in a relatively automatic fashion. Much research supports that the nucleus accumbens (NAcc), ventral tegmental area (VTA), prefrontal cortex (PFC), hippocampus, and subiculum form a loop that regulates goal-directed learning (see Lisman & Grace, 2005 for a review). Increased hippocampal activity signals novel stimuli that should receive attention. Activity in the NAcc and VTA increases in response to value cues, and this activity is thought to represent anticipation of rewards that influences goal-directed behavior (Adcock et al., 2006; Carter, MacInness, Huettel, & Adcock, 2009; Cohen, Rissman, Suthana, Castel, & Knowlton, 2014). The NAcc has also been shown to store reward prediction error information in probabilistic learning tasks (Chowdhury et al., 2013; Samanez-Larkin, Worthy, Mata, McClure, & Knutson, 2014). Dopaminergic neurons in the VTA modulate long-term potentiation in the hippocampus that is required for the maintenance of long-term memory (Bethus, Tse, & Morris, 2010; Rossato, Bevilaqua, Izquierdo, Medina, & Cammarota, 2009). This learning then allows the hippocampus to make more informed novelty judgements in future situations. Overall, this hippocampus-VTA loop allows rewarding items to be more strongly stored in long-term memory. Although activity in this loop is thought be modulating motivation,

effects of value on memory are also observed when value cues are presented after items are no longer present, suggesting that this dopaminergic enhancement of memory can occur when information is simply proximal to reward cues (Murayama & Kitagami, 2014). Chapter 3 presents research investigating whether strategic or automatic processes play a more prominent role in value-directed recognition.

1.4 Age-Related Neurological Changes and Value-Directed Remembering

Aging is accompanied by profound functional and structural changes in the brain. Research examining how functional changes in aging contribute to VDR is relatively limited and this is a topic in need of further investigation. One of the few studies on this topic includes Cohen et al. (2016), wherein older and younger participants completed a VDR task in an fMRI scanner. In their younger adult sample, which was first reported in Cohen et al. (2014), greater value-related selectivity was associated with value-based increases in activation in frontal regions (left inferior frontal gyrus and left middle frontal gyrus), temporal regions (middle and inferior gyri), and NAcc during word encoding. These frontal regions have been implicated in cognitive control and semantic processing (Badre & Wagner, 2007; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997), and NAcc activates in response to anticipated gains, losses, and punishment (Carter et al., 2009; Knutson, Adams, Fong, & Hommer, 2001); thus, younger adults likely used these regions to selectively encode valuable items. In contrast, older adults' selective encoding of valuable items is better supported by *decreased* activity in these regions while studying low-value items. These findings suggest that younger adults are more selective because they have more elaborate semantic processing of high-value items, whereas older adults reduce semantic processing for low-value items. Interestingly, Cohen et al. (2016) observed that in older adults there were no regions with greater activity for high-value cues than low-value

cues. Relative to older adults, younger adults showed increased activity in prefrontal, parietal, and occipital clusters in response to high-value cues, suggesting that value cues may be processed differently for younger and older adults.

Spaniol, Bowen, Wegier, and Grady (2015) also examined how processing of value cues changes in aging by presenting older and younger adults with a perceptual motor task and cues that they would earn either $5 or nothing for successful performance. Although younger adults had the same success rate as older adults, they earned more money. Additionally, only younger adults showed faster response times to rewarded versus unrewarded items. Their fMRI results indicated that younger adults deactivated default mode network areas in response to rewarded cues more than non-rewarded cues, whereas older adults showed increased activation in these areas. Considering the behavioral impairments older adults showed on rewarded items, this was likely dysfunctional activation in older adults, and the authors argued that the deactivation observed in younger adults likely reflected improved attention to high-value cues and items. Although older and younger adults often have similar memory for high-value items, the results of Cohen et al. (2016) and Spaniol et al. (2015) suggest that older and younger adults process reward cues in distinct ways.

These age-related functional changes in the brain are likely due to the profound structural changes that affect the brain in aging. Aging has been most strongly linked with declining volume and functioning of the frontal lobe and hippocampus (for review, see Gunning-Dixon et al., 2009), but recent research has implicated the thalamus as another important region that shrinks in aging. Anterior thalamic volume and frontothalamic tract integrity have been shown to degrade considerably in healthy aging (Fama & Sullivan, 2015; Hughes et al., 2012). The anterior thalamus is thought to be involved in declarative memory by selecting what information

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is stored and remembered (Van Der Werf, Jolles, Witter, & Uylings, 2003), thus age-related

frontothalamic tract degradation may result in changes to cognitive monitoring and efficient

selection of which stimuli get encoded. When examining age-related atrophy in these regions,

the Gunning-Dixon et al. (2009) review explains that grey matter is likely affected earlier and

more gradually, whereas white matter degrades more precipitously and at more advanced age.

Thus, measures of white matter atrophy and tissue damage may be particularly effective

predictors for cognitive changes that begin in old age. Gunning-Dixon et al. (2009) further

explained that white matter degradation in aging occurs through loss of myelinated fibers and

malformation of myelinated sheaths.

In addition to examining age-related structural changes within neural regions, it is

informative to examine changes in the structural connectivity between relevant regions, as

complex tasks such as VDR likely require integration of information across multiple regions.

Indeed, fMRI results suggest that VDR is supported by a diverse network of regions that show

value-based activation when participants view value cues and during word encoding (Cohen et

al., 2014; Cohen et al., 2016). Diffusion tensor imaging (DTI) is one of the most popular

techniques for estimating the structural integrity of white matter in neural regions and pathways.

In DTI, the directionality of the diffusion of water molecules is used to estimate white matter

structural integrity, and higher integrity allows for more efficient communication between neural

regions (see Assaf & Pasternack, 2008 for a review). White matter is fatty and insoluble to water,

thus water preferentially flows alongside it. Fractional anisotropy (FA) and mean diffusivity

(MD) are two of the most commonly used DTI measures. Within a voxel, higher FA scores and

lower MD scores both reflect a stronger preference for water to flow in a specific direction

(anisotropically) and generally indicate higher structural integrity. These measures reflect

different aspects of structural integrity, including axon density, diameter, and myelination (Beaulieu, 2002; Pierpaoli, Jezzard, Basser, & Barnett, 1996).

Although some research has examined how the structural integrity of white matter regions and tracts supports effective reward-based probabilistic learning (e.g., Chowdhury et al., 2013), relatively little research has examined the importance of this integrity to a more strategic VDR task. Such research may be particularly important in aging as DTI data may help us understand how structural changes and atrophy in the brain influence older adults' ability to selectively learn valuable information. Chapter 4 of this dissertation presents research investigating whether the structural integrity of various white matter regions and tracts supports effective value-related selectivity on a standard VDR task and whether older adults rely on different structures to learn selectively.

1.5 Overview of the Dissertational Studies

This dissertation is comprised of three studies developed to determine how VDR affects the quality of memory in aging, whether strategic or automatic processes play a bigger role in value's effect on memory, and whether individual differences in the quality of white matter regions and tracts explain differences in older adults' ability to selectively learn valuable material. The first study (Chapter 2) included two experiments designed to examine how VDR affects memory in younger and older adults. In the first experiment, participants completed a recognition memory task where studied words were worth different point-values. Participants earned those points later for correct recognition, which simulated that information differed in value. Responses of remembering, knowing, and guessing were collected to assess the subjective quality of their memory, and memory for incidentally encoded associated details (i.e., point-value and word color) was assessed. Our second experiment allowed us to observe whether value

effects we observed earlier would generalize to more naturalistic stimuli (pictures) and value manipulations (states of physiological need). We adapted our experimental design from Lin, Horner, Bisby, and Burgess (2015). In Experiment 2, younger adults and older adults imagined being in different locations and under different states of physiological need. Participants then viewed objects that were either congruent with that state of need (e.g., hungry & hamburger) or were not (e.g., hungry & water bottle), and then provided subjective judgments of how valuable the items were to them. They completed a recognition task with source memory questions (location and state of need). Executive functioning and working memory capacity were also examined, but these measures were not found to significant predict VDR performance in older adults. These null findings were not reported in the resulting manuscript to maintain conciseness.

In the second study (Chapter 3), two experiments were designed to determine what mechanisms supported VDR and whether these mechanisms were primarily strategic or automatic. The design for the first experiment was based on Gardiner, Gawlik, and Richardson-Klavehn's (1994) as they had an efficient manipulation to determine the influence of elaborative and maintenance rehearsal strategies in learning. The design involved a directed-forgetting paradigm where participants were told to either remember or forget each item, and yet they were tested on all items at the end of the study. Importantly, the directed-forgetting cue was presented with a variable delay that allowed us to compare performance between conditions that promoted elaborative encoding, maintenance rehearsal, or active forgetting. Maintenance rehearsal involves keeping the item in mind via rote repetition, and is indicative of merely increasing the encoding duration; this encoding type would best encapsulate differences in selective-attention. The effects of increased maintenance rehearsal were examined by comparing performance for items with a short versus long delay, whereas conditions that supported prolonged intentional

encoding were thought to also promote increased elaborative encoding. Contributions of

relatively automatic processes to VDR were examined with items paired with immediate forget

cues at encoding. In Experiment 2, instead of using a directed-forgetting design, we directly

instructed participants to use different encoding strategies while learning items that differed in

point-value. In three between-subjects groups, participants were given no instruction regarding

strategy use or they were instructed to learn all items using either a mental rehearsal or mental

imagery strategy.

In the third study (Chapter 4), DTI data were analyzed to determine if individual

differences in the microstructural integrity of white matter tracts predicted selective VDR in

older adults. We were particularly interested in the integrity of the IFOF due to its role in

semantic processing (Binder, Desai, Graves, & Conant, 2009; Binder & Desai, 2011) and the

NAcc-VTA pathway due to its role in modulating memory based on anticipated rewards (Carter

et al. 2009; Lisman & Grace, 2005). This study was based off a previously completed

experiment; younger adult fMRI data were collected and reported in Cohen et al. (2014),

whereas older adult fMRI data were previously reported in Cohen et al. (2016). In this

experiment participants completed a free recall VDR task where they learned words that differed

in point-value. They studied and were tested on multiple lists as this has been shown to promote

increased selective encoding (Cohen et al., 2017).

Chapter 2

The Effects of Value on Context-Item Associative Memory in Younger and Older Adults

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Valuable items are often remembered better than items that are less valuable by both older and younger adults, but older adults typically show deficits in binding. Here, we examine whether value affects the quality of recognition memory and the binding of incidental details to valuable items. In Experiment 1, participants learned English words each associated with a point-value they earned for correct recognition with the goal of maximizing their score. In Experiment 2, value was manipulated by presenting items that were either congruent or incongruent with an imagined state of physiological need (e.g., hunger). In Experiment 1, point-value was associated with enhanced recollection in both age groups. Memory for the color associated with the word was in fact reduced for high-value recollected items compared with low-value recollected items, suggesting value selectively enhances binding of task-relevant details. In Experiment 2, memory for learned images was enhanced by value in both age groups. However, value differentially enhanced binding of an imagined context to the item in younger and older adults, with a strong trend for increased binding in younger adults only. These findings suggest that value enhances episodic encoding in both older and younger adults but that binding of associated details may be reduced for valuable items compared to less valuable items, particularly in older adults.

2.1 Introduction

Remembering the past often involves remembering an event as well as the details associated with the event in question. Memory for associated details of an event requires the binding of information in memory, and there is evidence that older adults have impairments in associative memory (Old & Naveh-Benjamin, 2008). Although aging is associated with declines in free recall and recognition performance (Dulaney, Marks, & Link, 2004; Spaniol, Schain, & Bowen, 2014), it has been robustly shown that older adults are often as good as younger adults at remembering valuable material (Ariel, Price, & Hertzog, 2015; Castel, Benjamin, Craik, &Watkins, 2002; Castel et al., 2011; Cohen, Rissman, Suthana, Castel, & Knowlton, 2016; Spaniol et al., 2014). In the value-directed remembering (VDR) paradigm, each item is associated with a point-value that participants earn for retrieving the item at test—for example, ranging from 1 to 12 points—which simulates material differing in value. The ability to selectively learn valuable items is crucial for achieving a high score, as participants are presented with more information than they can possibly memorize. Effective VDR depends on attentional control, goal maintenance, and inhibition of less important information (Balota & Faust, 2001; Waszak, Li, & Hommel, 2010; Zelazo, Craik, & Booth, 2004). Despite extensive support that VDR is intact in healthy aging, less is known about whether value enhances binding of incidental details to valuable items. Furthermore, it is unclear whether the effects of value on memory in older adults are primarily attributable to selective encoding or would also be present when this selectivity is not incentivized. One possibility is that value enhances the binding of associated episodic details such that memory for these items will be accompanied by information in the study episode. On the other hand, valuable items may capture attention to the extent that less relevant information (such as the color of a studied word) is not encoded. If so, memory for

valuable items may be accompanied by fewer associated details. Although older adults may show similar VDR effects as younger adults, their effect of value on associative binding may differ between the two groups.

Formation of an episodic memory requires the binding of contextual details to the item. Several studies suggest that episodic memory is specifically impaired in older adults compared to memory based on feelings of familiarity that lack such binding (Koen & Yonelinas, 2014; Piolino et al., 2010). Although older adults have an impaired ability to encode or retrieve episodic details, paradoxically, they are also less able to ignore irrelevant details during encoding. Much research suggests that older adults are not as effective as younger adults at suppressing distracting information (Amer & Hasher, 2014; Healey, Hasher, & Campbell, 2013; Lustig, Hasher, & Tonev, 2006; Stevens, Hasher, Chiew, & Grady, 2008). Amer and Hasher (2014) had participants complete a Stroop task, followed by a test of general-knowledge. Half of the answers to the test were provided as distractors during the Stroop task. Interestingly, compared with younger adults, older adults showed substantially increased performance on questions related to the distractors, suggesting that they were not only having difficulty suppressing these conceptual distractors, but rather that they were semantically processing them. Taking this idea further, research has shown that older adults' encoding of distractors and irrelevant contextual information interacts with the encoding of target items, via a theory they termed hyper-binding (Campbell, Hasher, & Thomas, 2010; Campbell, Trelle, & Hasher, 2014). This increased encoding of distractors in older adults is measured by implicit measures such as priming. It is uncertain whether such hyper-binding would make older adults more likely to bind episodic details to valuable items as well.

In numerous studies, older adults have been shown to have deficits in source memory compared to younger adults that are disproportionate to any deficits in item memory (see Johnson, Hashtroudi, & Lindsay, 1993 for a review). Source monitoring in older adults may be particularly challenging when they must differentiate between perceptual characteristics of possible sources (e.g., the spatial location of a stimulus, or which speaker had read the study item; Kausler & Puckett, 1981; Light & Zelinski, 1983; but see also Rahhal, May, & Hasher, 2002). Older adults appear to perform better on source monitoring tasks in which the sources differ in terms of the amount of cognitive operations performed (imagining a task vs. actually performing the task; Hashtroudi, Johnson, & Chrosniak, 1989). It is possible that the greater difficulty with source memory dependent on perceptual details reflects a deficit in binding these arbitrary details to items during encoding, and that this reduced binding may serve to direct attention to the item itself as a means to compensate for reduced memory. Item value may thus not attenuate this age related deficit in binding source details, but rather, may lead to greater focus on item memory at the expense of source details.

In contrast, other evidence suggests that older adults are able to bind contextual details to items during encoding, as older adults are able to use these details to cue item retrieval, and they benefit as much as younger adults when study and test context are identical (Naveh-Benjamin & Craik, 1995). These findings suggest that aging may not decrease contextual binding, but that older adults may have more difficulty explicitly accessing these memories by inducing the original context at test. This interpretation aligns with the view of Craik (1986) that older adults show deficits in self-initiated memory processes due to reduced cognitive resources. Mentally reinstating study context is likely resource demanding, while benefitting from congruence of contextual details at study and test does not require self-initiated processes. If value affects the

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binding of contextual details to valuable items, it may be that older adults would still show deficits in memory for these details due to difficulty reinstating these details at test. Thus, current views of encoding contextual detail memory in older adults do not provide a strong hypothesis regarding the effects of value on memory for these details.

One focus of the present study was to determine how value shapes the quality of memory, in terms of the degree of recollection versus familiarity, and the level of source memory detail in younger and older adults. The role of value in episodic binding has received limited research, especially for older adults. Hennessee, Castel, and Knowlton (2017) observed across three recognition experiments that younger adults more frequently experienced recollection (Remember responses) for retrieved high-value items, though there was little if any effect of value on familiarity. Additionally, recollected high-value items were more likely to be bound to the task-relevant point-value of an item but less likely to be bound to task-irrelevant word color than nonrecollected high-value items. This suggests that high-value items are encoded at a deeper level, perhaps via elaborative semantic encoding, and that value can influence the binding of episodic details. Value appears to reduce binding of task-irrelevant information in younger adults. Given that older adults show impairments to episodic memory (Koen & Yonelinas, 2014) value may not enhance recollection to the same extent as in younger adults. Additionally, does value affect binding of incidental details to studied items, and is any effect on binding similar for younger and older adults?

We were also interested in whether the effect of value on memory in older adults is based on strategic processing, or if it occurs relatively automatically. Selectively encoding valuable items in the VDR procedure appears to rely on shifting one's strategy use depending on the value of the item. In Ariel, Price, and Hertzog (2015) both older and younger adults used more

effective learning strategies for high-value word pairs, including generating an image or word that mediated the relationship between the word pair, putting the word pair into a sentence, or thinking about how the word pair was semantically related. For both age groups, these encoding strategies improved retrieval relative to rote memorization. Another commonly used and effective strategy is to avoid attending to low-value items (Ariel et al., 2015; Robison & Unsworth, 2017). Ignoring low-value items is beneficial because when not all items can be memorized, reward is maximized when cognitive resources are devoted to high-value items. In most value and reward-based learning studies, there are incentives (e.g., money or point-values) and recommended goals (e.g., maximize score) to encourage such strategic encoding. In Experiment 2 we sought to measure whether older adults will show similar effects of value on memory when they are not engaging in strategic encoding. In support of more automatic effects of value at encoding, high-value cues have been shown to attract attention in an involuntary manner (Anderson, 2013; Hickey, Chelazzi, & Theeuwes, 2010). Unlike Experiment 1, in which value was manipulated by point-value, in Experiment 2, value was inherent to study items based on an imagined state of need (e.g., a blanket when imagining being cold) and encoding valuable items was not incentivized. Thus, this second experiment used a more naturalistic manipulation of value in an attempt to extend our results.

2.2 Experiment 1

Experiment 1 was designed to determine whether value affects the quality of recognition memory and associative binding of incidental details in younger and older adults. At study, each item was presented in one of four different colors and was associated with a point-value that would be earned for correct recognition. At test, for each item the participant deemed "old," they reported whether they recognized the item through remembering, knowing, or guessing (R-K-G)

and then what color and point-value they believed were associated with the item at study. Remember and Know responses require the participant to introspect whether recognition was based on recollection of the study episode for the item or if they simply knew the item was presented before because of a strong sense of familiarity. A Guess response was included because subjects sometimes use the Know response as a proxy for guesses when no alternatives are explicitly allowed (Gardiner, Java, & Richardson-Klavehn, 1996), and the current task was relatively difficult. Both R-K-G responses and incidental detail retrieval were assessed to better determine whether value affects the overall quality of memory or memory for specific episodic details associated with the studied item.

First, we hypothesized that both older and younger adults would exhibit a value effect on memory with high-value items receiving a higher hit rate. This would follow a large literature demonstrating that VDR is preserved in healthy aging (Ariel et al., 2015; Castel et al., 2002, 2011; Cohen et al., 2016; Spaniol et al., 2014). Second, we hypothesized that high-value items would be associated with increased recollection for younger adults, but possibly not for older adults. We have previously observed that younger adults consistently show enhanced recollection of high-value items (Hennessee et al., 2017). Because older adults show impairments to episodic memory and rely more on familiarity during retrieval (Koen & Yonelinas, 2014; Piolino et al., 2010) we did not expect them to necessarily use recollection to the same extent. Third, we hypothesized that older adults would show less binding of incidental details with studied high value items at encoding, given previous work suggesting that older adults may not acquire incidental source information as well as younger adults (Johnson et al., 1993). Older adults may selectively allocate attentional resources to the valuable items at the

expense of encoding incidental details. However, it is also possible that value could enhance binding of source details to items similarly for both age groups.

2.3 Method

    2.3.1 Participants. Data from 33 older adults (18 women and 15 men) from Los Angeles were collected for this study. The age range was 59–91 (M = 77.44, SD = 7.51). Participants were required to have had no prior diagnosis of memory disorder (e.g., dementia), and they were in good health (M = 8.10, SD = 1.60) on a scale from 1 (poor health) to 10 (excellent health). The highest level of education achieved was college (n = 16), graduate school (n = 15), or high school (n = 1). Participants were paid $10 per hour of participation. Data from 33 undergraduate students (22 women and 11 men) from University of California, Los Angeles (UCLA) were collected as a cross-sectional comparison group. Their age range was 18–28 (M = 20.68, SD = 2.30). These participants completed the study for course credit. Informed consent was acquired and the study was completed in accordance with UCLA's Institutional Review Board. All older and younger adults were fluent in English with no self-reported color blindness.

    2.3.2 Materials. Stimuli consisted of 96 English words, including nouns, adjectives, and verbs. During encoding, 48 of these words were randomly presented and paired with a point-value of 1, 2, 3, 10, 11, or 12 presented to the right of the word (e.g., "rivers 3"). These values were chosen to maximize the difference between words with low (1-3pt.) and high (10-12pt.) value. Each word was printed in one of four ink colors: red, yellow, lime green, or cyan blue. Four colors were used as these were the most distinct colors in the e-prime presentation software. Participants were not asked to memorize the point-value or word color, as these were later used to assess incidental memory. Words had a mean frequency of 4466.12 (*SD* = 237.11) occurrences per million in the Hyperspace Analogue to Language corpus (Lund & Burgess,

1996), and whether a word was designated as low-value, high-value, or a distractor was counterbalanced. During the recognition test, all 96 words— half that were presented at study and half that were new—were presented randomly, without their point-value and printed in white. All materials were presented on a desktop computer running Windows 7. All words were printed in 18 pt., Courier New font with a black background. The study was programmed onto the computer and data were recorded using e-prime (ver. 2.0) software with a keyboard.

2.3.3 Procedures. Participants completed the study individually. They were instructed that they would view a large set of words, each associated with a point-value they could earn later for recognition. They were told that their goal was to maximize their score. All 48 study items were presented individually for 3 s per word with a 0.5-s fixation cross between words. Next, participants completed a brief distractor task to reduce mental rehearsal, which consisted of seven simple multiplication and division problems. Before starting the recognition test, the meanings of the terms "Remember," "Know," and "Guess," were explained using an adapted form of Gardiner and Java's (1990) instructions (see the Appendix). Each participant was asked what they believed it meant to remember a word, and for inadequate responses, the experimenter gave further instruction.

The recognition test was self-paced, and participants were informed that they would lose 2 points for incorrect responses to discourage the otherwise optimal strategy of labeling all items as "old." Participants first reported how certain they were that each word was presented before on a 6-point scale: 1 "Definitely NEW," 2 "Probably NEW," 3 "Maybe NEW," 4 "Maybe OLD," 5 "Probably OLD," or 6 "Definitely OLD." After choosing any of the three "old" responses, they further reported whether they recognized the item due to remembering, knowing, or guessing. Next, they were asked what point-value each item was initially associated with, and

what color it was printed in, with possible choices listed on the screen. When items were rated

"new," they completed a filler question where they rated the pleasantness of the word.

2.3.4 Data Analysis. Data were analyzed using SPSS (ver. 23) and ANOVAs were

Greenhouse-Geisser corrected. Words worth 1–3 points were considered low-value, whereas

those worth 10–12 were high-value. Prior to analysis, for younger and older adults separately,

the fastest and slowest 2.5% of recognition trials were excluded. In line with advice by Ratcliff

(1993) these criteria were chosen to eliminate the small proportion of responses that may have

had abnormally high or low response times (RTs) attributable to factors such as a participant

needing procedural clarification or a participant blindly making a quick response to progress

through the study quickly. The proportion of excluded trials did not significantly differ across

new, low-value, and high-value items for younger adults, $F(2, 20) = 2.78$, $p = .086$, or older

adults, $F(2, 12) = 1.57$, $p = .249$.

Three older adults were excluded from color retrieval analyses, because they showed no

variance in color response. Two younger adults and four older adults were excluded from

analyses examining R-K-G responses, as their false alarm rate for remembered items was over

two standard deviations above the average for younger adults ($M = .11$, $SD = .18$), and older

adults ($M = .23$, $SD = .33$), respectively.

To examine recognition performance, signal detection measures A_z and B_D'' were used.

Recognition sensitivity, A_z, measures one's ability to distinguish old items from new items, and

ranges from 0 to 1, with chance performance at 0.5. Unlike most recognition performance

measures, A_z is largely unaffected by response bias, and is computed as the area under a

cumulative hit versus false alarm rate curve where each confidence response from highest to

lowest is treated as a "yes" response (Stanislaw & Todorov, 1999). B_D'' is a measure of response bias computed using hit and false alarm rates, with positive values here indicating a bias toward labeling an item as new (Donaldson, 1992).

2.4 Results

2.4.1 Value Effects on Recognition Performance. Older adults recognized a significantly smaller proportion of words than younger adults, $t(64) = -2.96$, $p = .004$, $d = -0.73$ (see Table 2.1). However, the false alarm rates of older adults and younger adults did not significantly differ, $t(64) = 0.82$, $p = .413$, $d = 0.20$. This difference in hit rate resulted in older adults having a significantly lower recognition sensitivity (A_z) than younger adults, $t(64) = -3.25$, $p = .002$, $d = -0.82$. Response bias (B_D'') was not found to be significantly different between older and younger adults, $t(64) = -0.06$, $p = .955$, $d < -0.01$. Both groups had a slight bias to label items as new.

To determine the effects of value and age group on recognition, a 2×2 repeated measures ANOVA was computed (see Table 2.1). A Significant Value × Age Interaction was observed, $F(1, 64) = 5.35$, $p = .024$, $\eta_p^2 = .77$. Post hoc analysis revealed that younger adults were significantly more likely to recognize low-value items than older adults, $t(64) = 3.48$, $p = .001$, $d = 0.86$. However, the hit rate to high-value items was not significantly different between younger adults and older adults, $t(64) = 1.58$, $p = .119$, $d = 0.39$. Similarly, a Value × Age Interaction for recognition confidence was observed, $F(1, 64) = 4.87$, $p = .031$, $\eta_p^2 = .71$. Post hoc analysis revealed, older adults had significantly higher confidence ratings for high-value items than for low-value items, $t(32) = 4.68$, $p < .001$, $d = 0.81$. In contrast, younger adults confidence did not significantly differ between high-value and low-value items, $t(32) = 1.27$, $p = .213$, $d = 0.22$. Still, even for high-value items, younger adults had higher confidence ratings than older adults,

$t(64) = 2.40$, $p = .019$, $d = 0.59$. Younger ($M = 2.67$, $SD = 0.57$) and older adults ($M = 2.71$, $SD = 0.65$) did not significantly differ in their confidence to new items, $t(64) = −0.26$, $p = .792$, d = −0.07. The total number of points earned in the study significantly differed between older adults ($M = 178.03$, $SD = 54.39$) and younger adults ($M = 203.79$, $SD = 48.50$), $t(64) = −2.03$, $p = .046$, $d = −0.50$. Thus, older adults' reduced hit rate was primarily due to impaired memory for low-value items, and their memory for high-value items was largely intact.

Table 2.1 Experiment 1 Recognition Test Results

	Younger Adults		Older Adults	
Hit rate	.68 (.15)		.56 (.17)	
False alarm	.24 (.15)		.27 (.16)	
A_z	.78 (.12)		.69 (.10)	
B''_D	.16 (.33)		.16 (.26)	
RT (ms)	3279 (528)		6697 (2216)	
	Recognition by Item Value			
	Younger Adults		Older Adults	
	Low-Value	High-Value	Low-Value	High-Value
Hit rate	.67 (.18)	.68 (.16)	.51 (.21)	.62 (.17)
Confidence	4.31 (0.71)	4.47 (0.65)	3.53 (0.75)	4.07 (0.72)
R	.40 (.24)	.52 (.25)	.33 (.22)	.49 (.26)
K	.24 (.16)	.23 (.15)	.23 (.25)	.23 (.23)
G	.36 (.26)	.26 (.24)	.43 (.25)	.28 (.24)

Note. Standard deviations presented in parentheses. A_z =recognition sensitivity, B''_D = response bias, RT = response time, R = proportion Remembered, K = proportion Known, G = proportion Guessed

2.4.2 Value and Experiences of Remembering, Knowing, and Guessing. To determine whether age or value were associated with differences in experiences of recollection, a repeated measures Age × Value × Memory Type (R-K-G) ANOVA was computed. The three-way interaction and all analyses involving age group were not found to be significant ($p \geq .545$). A significant value × memory type interaction was observed, $F(1, 58) = 11.58$, $p = .001$, $\eta_p^2 = .17$. Post hoc analysis indicated that a significantly greater proportion of high-value items ($M = .50$, $SD = .25$) received a Remember response than low-value items ($M = .37$, $SD = .23$), $t(59) = 4.80$,

$p < .001$, $d = 0.62$. In contrast, the proportion of items given a Know response did not

significantly differ between high-value ($M = .23$, $SD = .19$) and low-value items ($M = .24$, $SD =$

.21), $t(59) = -0.30$, $p = .766$, $d = -0.04$. Guessing was significantly more prevalent for low-value

items ($M = .39$, $SD = .26$) than high-value items ($M = .27$, $SD = .24$), $t(59) = 4.65$, $p < .001$, $d =$

0.56.

2.4.3 Incidental Detail Retrieval. When examining color retrieval for correctly

recognized items, the Age × Memory Type (Remember or Know) × Value Interaction was not

found to be significant, $F(1, 38) = 0.12$, $p = .730$, $\eta_p^2 < .01$, and age group had no main effect or

interactions with other variables in this analysis ($p \geq .239$). A Significant Value × Memory Type

interaction was observed, $F(1, 38) = 4.36$, $p = .044$, $\eta_p^2 = .10$ (see Figure 2.1). Specifically,

participants were more likely to retrieve the color of known high-value items ($M = .32$, $SD = .31$)

than remembered high-value items ($M = .19$, $SD = .17$), $t(48) = 2.40$, $p = .020$, $d = 0.36$; this

difference was not significant for remembered and known low-value items, $t(40) = 1.72$, $p =$

.093, $d = 0.27$. Interestingly, for Remember responses, there was a higher color retrieval rate for

low-value items ($M = .36$, $SD = .30$) than high-value items ($M = .20$, $SD = .17$), $t(54) = 3.29$, $p =$

.002, $d = 0.46$; this difference was not significant for Know responses, $t(41) = 0.61$, $p = .545$, $d =$

0.09. Overall retrieval of word color for both groups was not significantly different from chance

($p \geq .461$), though low-value Remember responses were associated with memory for the

associated color at a level above chance performance ($p = .007$). Thus, recollection of high-value

items was associated with a decrease in color retrieval compared to recollection of low-value

items.

When examining point-value retrieval for recognized items, the Age × Memory Type ×

Value Interaction was not found to be significant, $F(1, 38) = 3.69$, $p = .062$, $\eta_p^2 = .09$. Likewise,

age group did not produce a significant main effect or any interactions ($p \geq .291$). A main effect of memory type was observed, such that correct point-value retrieval was significantly more likely after a Remember response ($M = .20$, $SD = .18$) than a Know response ($M = .11$, $SD = .15$), $F(1, 38) = 6.24$, $p = .017$, $\eta_p^2 = .14$. Although the three-way interaction was not statistically significant, it may bear mentioning that only younger adults showed a value × memory type interaction, $F(1, 25) = 5.53$, $p = .027$, $\eta_p^2 = .18$. Specifically, although younger adults more often retrieved high values through remembering than knowing, $t(29) = 3.48$, $p = .002$, $d = 0.67$, this difference was not significant in older adults, $t(20) = 0.95$, $p = .352$, $d = 0.21$. One limitation of this analysis was that participants were allowed to manually enter their response, and some reported point-values not used in this study (e.g., 6-points). The proportion of point-value responses that were invalid—anything except 1, 2, 3, 10, 11, or 12—was not significantly different between remembered ($M = .33$, $SD = .29$) and known ($M = .40$, $SD = .32$) items, $t(52) = -1.60$, $p = .117$, $d = -0.21$, suggesting that the above memory type effect was not solely due to a difference in invalid responding. When only valid point-value responses were examined, both age groups were more accurate than chance for recollected items ($p \leq .010$).
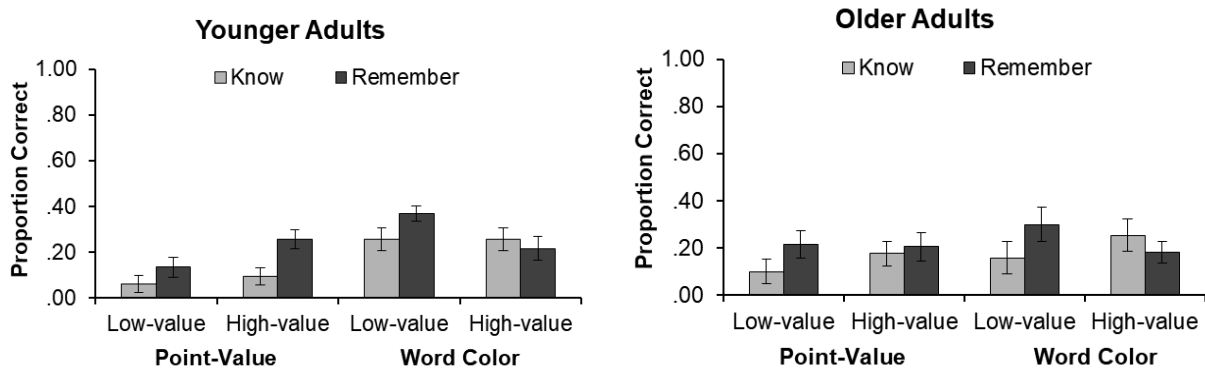
Figure 2.1. Incidental detail retrieval by word value and memory type (Remember or Know) for Experiment 1. Error bars represent one standard error from the mean.

2.5 Discussion

The results of the current study support prior work that shows that older adults show impaired recognition relative to younger adults in a value-based memory task (cf. Castel, Farb, & Craik, 2007; Spaniol et al., 2014). Although older adults typically show an increased false alarm rate (Jacoby, 1999; Spaniol et al., 2014) in these types of tasks, the penalty for false alarms on this task may have led them to respond more conservatively. Consistent with our first hypothesis, high-value items were better recollected for both younger and older adults. Older adults show intact effects of value, using free recall (Ariel et al., 2015; Castel et al., 2011), and the current findings suggest that this also applies to recollection. Furthermore, in older adults, value was associated with increased confidence, suggesting that selectively encoded valuable items results in stronger memory traces. As previously observed with younger adults (Hennessee et al., 2017), high-value items were more likely to be recollected at test, and value did not have a substantial effect on knowing. These findings suggest that the relationship between value at encoding and increased recollection at retrieval may be relatively preserved in healthy aging.

Contrary to our second hypothesis, this benefit of value to recollection was intact in healthy older adults. Our third hypothesis, that older adults would show impaired binding of contextual information to valuable items, was not supported. The effects of value on memory for incidental details were similar for younger and older adults. Interestingly, although remembering was associated with more point-value retrieval, for word color there was a Value $\times$ Memory Type interaction such that recollected valuable items showed less retrieval. Point-value was a highly relevant detail on this task, so this detail may have been bound to well-encoded items. In contrast, word color was irrelevant to task performance, so when selectively encoding valuable items, participants may have focused on the item itself at the expense of encoding this detail.

These findings are consistent with our previous work showing that although value increases

recollection, it appears to decrease memory for irrelevant details associated with the studied item

(Hennessee et al., 2017). These results are also generally consistent with the Arousal Based

Competition (ABC) framework (Mather & Sutherland, 2011), in which arousal biases

competition to encode high priority information at the expense of less important information.

According to this framework, value may bias this competition, either based on top-down

attention to the relevant aspects of valuable stimuli or on automatic increased salience of these

stimuli at the expense of irrelevant dimensions. The present results extend this finding to older

adults. Value may serve to focus attention on task-relevant information.

2.6 Experiment 2

To determine how value effects in healthy aging generalize to more naturalistic value

judgments and stimuli, stimuli and methods were adapted from Lin, Horner, Bisby, and Burgess

(2015). Lin et al. (2015) observed that younger adults had better memory for physiologically

valuable items in imagined scenarios, but it was uncertain whether this form of value would also

affect older adults' memory for items and item-context associations. Participants imagined being

in different states of physiological need (e.g., hunger) and in different locations, then receiving

two items sequentially. By examining both the congruency of the item with the state of need and

participants' ratings of item value, we could dissociate whether value effects on recognition were

due to the manipulation or to participants' appraisals of value. Unlike the point-values used in

Experiment 1, value was manipulated here as an inherent property of the item. It is possible that

older and younger adults will differ in terms of the effects of value on memory when they are not

strategically attempting to maximize their score.

We predicted that both age groups would be more likely to recognize valuable items, showing that recognition memory can be enhanced by more naturalistic rewards. We also predicted that older adults would have worse retrieval than younger adults for the associated context for valuable items, as they may selectively allocate attentional resources to valuable items at the expense of this arbitrary detail. As in Experiment 1, it may be that value focuses attention on valuable items at the expense of context. On the other hand, the imagined context could lead to generation of semantic associations with the item which would lead to better memory for the context of high value items.

2.7 Method

2.7.1 Participants. Data from 30 older adults (10 women and 20 men) from Los Angeles were collected for this study. The age range was 62–92 ($M = 78.43$, $SD = 7.40$). This sample had no reported diagnoses of dementia, and a high self-reported health ($M = 7.63$, $SD = 1.69$). The highest level of education reported was college ($n = 11$), graduate school ($n = 18$), or unreported ($n = 1$). Participants were compensated \$10 per hour of participation. Nine participants had participated in Experiment 1 and our pattern of results was largely unchanged when excluding these participants (Supplemental Material).

Data from 30 undergraduate UCLA students (17 women and 13 men) were used for cross-sectional comparison. Their age range was 18–25 ($M = 20.53$, $SD = 1.68$). They completed the study for course credit, and procedures conformed to the UCLA Institutional Review Board guidelines. All participants were fluent in English.

2.7.2 Materials and Design.

2.7.3 Imagery Task. During the encoding task, participants imagined being in one of four states of physiological need (hunger, thirst, cold, or tired) and in one of four locations (beach,

kitchen, forest, or fields). No state-context combination was repeated. In four trials, a neutral condition was included where the subject was in no state of need. Instructions for neutral condition: "Imagine that you are just fine. You are not in any state of need, but just in an ordinary condition." Neutral trials allowed for examination of memory performance when value was not manipulated. Next, they viewed two images sequentially. Stimuli included 60 pictures of common items divided evenly into four categories meant to alleviate only one of the four states of need. These four categories included: food, drink, warmth-providing items (e.g., sweater, scarf), and items used for rest (e.g., bed, bath tub). Each presented item could either be congruent or incongruent with the current state of need. A congruent item represents something that helps alleviate that state of need, and should thus be valuable. In contrast, an incongruent item would not alleviate the need, making it low-value. These images were presented at a resolution of 130 130 on a white background. The item set was shortened from Lin et al. (2015) to avoid overtaxing older adult participants.

Forty images were presented at study. The recognition test included half of the items from the study phase, and the remaining 20 new items for a total of 40 items. Whether each item was presented at study or only at test was counterbalanced, and the order of images during both phases was randomized. Additionally, the order of which items on a trial were congruent or incongruent was counterbalanced, so that the effect of congruency was not confounded with item order. This study was programmed with e-prime software (ver. 2.0) on a Windows 7 desktop computer.
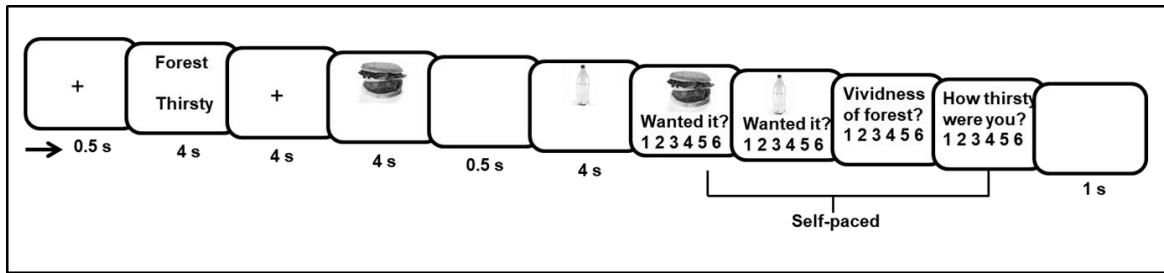
Figure 2.2. Study phase trial design (Experiment 2). Images courtesy of winnond and Suat Eman at FreeDigitalPhotos.net.

2.7.4 Procedures. Participants completed the study individually. Each imagery trial began with a 0.5 s fixation cross, followed by the location-state cue (e.g., thirsty in a forest) for 4 s, followed by another fixation cross for 4 s (see Figure 2.2). During the location-state presentation and fixation cross, participants were instructed to imagine being in the presented location with the state of need. Next, they saw two objects sequentially for 4 s each, with a 0.5-s blank screen in-between. Participants were instructed to imagine having the object, but not consuming it to alleviate their imagined need. To assess subjective value, each item was presented at the top of the screen and they reported how much they wanted it on a 6-pt scale (not very much to very much). They then used that scale to rate how vividly they imagined the location and state of need. For these questions, the relevant item was displayed and completion was self-paced. This was followed by a 1-s blank screen before the next trial began. The study phase consisted of 20 trials with 4 trials having a neutral state of need.

Next, participants completed 20 simple multiplication and division problems as a distractor task. During the recognition test, participants were shown each of the 40 test images randomly and asked whether they imagined the item earlier (yes/no) and how confident they were on a 6-pt confidence scale ranging from 1 "Definitely NEW" to 6 "Definitely OLD" (same as Experiment 1). For items rated "old," they indicated which location was previously associated

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with the item, with possible choices listed on the screen. This procedure was not used to assess state memory, as participants typically choose a state that is congruent with the item (Lin et al., 2015). Instead, participants were presented with one of the states of need and rated whether they imagined that state with that item. Due to an error in the randomization, these data were not suitable for analysis. When items were rated "new," they instead completed a filler question where they rated how much they usually like the item. There was a 0.5-s fixation cross separating each test trial.

 2.7.5 Data Analysis. To examine the relationship between objective value, subjective value, and age group on recognition and incidental detail retrieval, repeated measures ANOVAs with Greenhouse-Geisser corrections were computed. Significant interactions were followed by post hoc t tests. Because only eight items had the state of need as neutral, no comparisons were planned for these items. Because of the relatively low trial count, we did not use a reaction time (RT) trim, like in Experiment 1. One older adult was excluded from subjective value analyses, because he or she gave all items a 1 rating, and another was excluded from confidence analyses for using the scale incorrectly.

2.8 Results

 2.8.1 Value Effects on Recognition Performance. Recognition performance was high, with no significant difference in hit rates between older and younger adults, $t(58) = 0.35$, $p = .731$, $d = 0.09$ (see Table 2.2). However, older adults had a significantly higher false alarm rate than younger adults, $t(58) = 2.70$, $p = .009$, $d = 0.70$. This increased false alarm rate led older adults to have a lower recognition sensitivity, A_z, than younger adults, $t(57) = -2.66$, $p = .012$, $d = -0.79$. The response bias measure, B''_D, was lower for older adults than younger adults, $t(58) = -2.76$, $p = .008$, $d = -0.71$, as older adults were slightly biased to label items as "old."

Table 2.2 Experiment 2 Recognition Test Results

	Younger Adults	Older Adults
Hit rate	.82 (.18)	.84 (.20)
False alarm	.13 (.17)	.26 (.20)
A_z	.91 (.05)	.83 (.17)
B''_D	.16 (.56)	-.24 (.56)
RT (ms)	2580 (837)	4415 (1327)

	Recognition by Item Value			
	Younger Adults		Older Adults	
	Low-Value	High-Value	Low-Value	High-Value
Objective Value				
Hit rate	.78 (.21)	.88 (.20)	.82 (.24)	.87 (.19)
Confidence	5.03 (0.80)	5.44 (0.45)	4.89 (1.14)	5.16 (1.15)
Subjective Value				
Hit rate	.80 (.22)	.86 (.21)	.79 (.26)	.85 (.18)
Confidence	5.15 (0.84)	5.29 (0.60)	4.95 (1.09)	5.17 (1.21)

Note. Standard deviations presented in parentheses. A_z = recognition sensitivity, B''_D = response bias, RT = response time. Objective value congruency is presented:incongruent (low-value) and congruent (high-value).

To examine whether the congruency of an item with its state of need— our measure of objective item-value—and age were related to recognition performance, a 2×2 repeated measures ANOVA was computed. The main effect of congruency was significant, as the hit rate was higher for valuable (congruent) items ($M = .88$, $SD = .19$) than incongruent items ($M = .80$, $SD = .22$), $F(1, 58) = 9.29$, $p = .003$, $\eta_p^2 = .14$. The main effect of age group was not significant, nor was the interaction ($p \geq .222$). A 2×2 repeated measures ANOVA examining congruency and age's relationship with confidence in retrieval also revealed a significant main effect of congruency such that valuable items ($M = 5.37$, $SD = 0.70$) were more confidently recognized than incongruent items ($M = 5.03$, $SD = 0.85$), $F(1, 57) = 11.78$, $p = .001$, $\eta_p^2 = .17$. The main effect of age and interaction were not found to be significant ($p \geq .520$). Thus, for both age groups, items that were valuable based on imagined state of need were selectively encoded, resulting in enhanced retrieval at test. Additionally, value resulted in increased confidence, suggesting that there was a stronger memory trace for valuable items.

The effects of high (5– 6) and low (1–2) subjective value and age on hit rates were examined using a 2×2 repeated measures ANOVA. A significant main effect of subjective value was observed, as items with high subjective value ($M = .86$, $SD = .20$) were better recognized than low-value items ($M = .80$, $SD = .24$), $F(1, 55) = 5.51$, $p = .023$, $\eta_p^2 = .09$. The effect of age and interaction were not significant ($p \geq .812$). The number of items given a high subjective value rating did not significantly differ between younger ($M = 6.50$, $SD = 2.49$) and older adults ($M = 6.56$, $SD = 3.27$), $t(57) = -0.07$, $p = .946$, $d = -0.02$, though older adults gave more low ratings ($M = 9.00$, $SD = 3.78$) than did younger adults ($M = 7.13$, $SD = 2.33$, $t(57) = 2.29$, $p = .026$, $d = 0.61$. A 2×2 ANOVA examining subjective value and age showed that subjective value did not have a significant main effect on confidence, $F(1, 54) = 2.45$, $p = .124$, $\eta_p^2 = .04$. To examine whether subjective value varied predictably with objective value, a 2 (congruency) $\times$ 2 (age) ANOVA was computed. As expected, items congruent with the state of need ($M = 4.51$, $SD = 0.99$) received significantly higher subjective value ratings than incongruent items ($M = 2.42$, $SD = 0.75$), $F(1, 57) = 192.62$, $p < .001$, $\eta_p^2 = .77$. Overall, these results suggest that both the objective and subjective value of an item enhanced recognition, though only objective value was reliably associated with higher confidence. Furthermore, although older adults had worse overall recognition memory, both age groups exhibited these value-based enhancements of memory and performed comparably for items deemed valuable.

2.8.2 Value and Context Retrieval. When examining the proportion of trials with correct location retrieval, the main effect of age showed a strong trend, as younger adults ($M = .42$, $SD = .14$) were numerically more likely to retrieve the location than older adults ($M = .34$, $SD = .15$), $F(1, 57) = 3.93$, $p = .052$, $d = 0.55$. Both groups performed better than chance ($p \leq .003$). Additionally, an Age X Objective Value Interaction was observed, $F(1, 57) = 6.58$, $p = .013$, η_p^2

= .10 (see Figure 2.3). Post hoc *t* tests revealed that younger adults showed a strong trend to better remember the imagined location associated with items congruent with the state of need than incongruent items, $t(29) = 1.97$, $p = .058$, $d = 0.36$. In contrast, older adults showed a weak trend for better memory for imagined contexts on trials in which objects were incongruent with imagined need compared with valuable items, $t(28) = 1.74$, $p = .093$, $d = 0.32$. Older adults' location retrieval was similar to that of younger adults for incongruent items, $t(57) = 0.16$, $p = .873$, $d = 0.06$, but older adults showed markedly lower context retrieval for valuable items, $t(57) = 2.98$, $p = .004$, $d = 0.78$. Thus, value may have strengthened the item-context association in younger adults, though it did not benefit older adults, and may have even reduced binding.
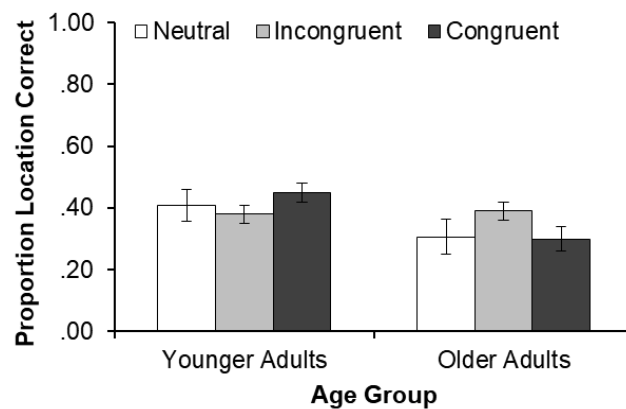
Figure 2.3. Proportion of correctly recognized items with their associated location retrieved at test by value and age group for Experiment 2. Error bars represent one standard error from the mean.

2.9 Discussion

Overall, these findings suggest that value effects on memory in older adults extend to more naturalistic stimuli and appraisals of value (i.e., physiological need) and can occur without any incentive for strategic encoding. In support of our first hypothesis, both age groups were more likely to recognize objectively and subjectively valuable items at test, extending previous work with memory tasks using arbitrary point-values. Subjective value ratings varied

considerably, but in support of the value manipulation, congruent items received substantially higher ratings than incongruent items. A dissociation was observed between these two measures of value on recognition confidence, such that objective value, but not subjective value, was associated with greater confidence at recognition. Our second hypothesis, that older adults would show impaired context-item binding for valuable items, was supported. Younger adults showed a strong trend for increased binding between context and item for valuable items, whereas older adults did not show such a benefit, and in fact showed a numerical reduction in context memory for valuable items. One possible contributor to these results could be differences in mental imagery or arousal in older adults that impacted encoding of the context. However, the fact that older and younger adults showed similar effects of congruency with an imagined state of need suggests that older adults performed this aspect of the task successfully. It may be that older adults had more difficulty imagining the associated contexts at study. But, this would more likely result in only a main effect of age group, while the more interesting finding was the interaction with value and group. These results suggest that value is having different effects on encoding the imagined context in younger and older adults. Research has shown that older adults have worse memory for associated details (Ariel et al., 2015; Koen & Yonelinas, 2014), and the current findings illustrate that this deficit may be more prominent when encoding valuable items. Value may direct attention away from associated details, particularly for older adults, resulting in enhanced encoding of the valuable items.

2.10 General Discussion

In two experiments, we examined how value shapes the quality of recognition memory in younger and older adults. Whether value at encoding consisted of an associated point-value, congruency with a state of imagined physiological need, or subjective value rating, valuable

items were better recognized or recollected. Thus, value effects generalize robustly to somewhat more naturalistic stimuli and measures of value. According to ABC theory (Mather & Sutherland, 2011), the amygdala modulates a frontoparietal memory network to selectively enhance processing of goal-relevant, and thus important, stimuli. It is likely that this goal-dependent modulation of memory processing also accounts for much of the value effects on memory observed in this study. Using the similar materials and procedure as Experiment 2, Lin et al. (2015) observed that amygdala activity at encoding correlated with successful retrieval. Our results suggest that this modulation by the amygdala may be relatively intact in older adults. Although older adults displayed worse recognition memory in both experiments, their ability to remember valuable items was comparable to younger adults. This supports a wide literature suggesting that value enhanced remembering is preserved in healthy aging (e.g., Ariel et al., 2015; Spaniol et al., 2014). With older adults' more limited memory, selectively encoding valuable items appears to be an adaptive strategy.

Given that older adults display robust enhancement of memory by value, the next question is what effect value has on the quality of their memory. In Experiment 1, both age groups had substantially increased remembering, but not knowing, for valuable items. This dissociation suggests that selectively encoding valuable items improves recognition primarily through enhancing recollection. We have observed that younger adults show increased recollection, but not familiarity, for valuable items (Hennessee et al., 2017), but we did not necessarily expect this to occur for older adults, as they generally exhibit episodic memory deficits (Koen & Yonelinas, 2014; Piolino et al., 2010). The current findings suggest that value promotes older adults' use of recollection during recognition. In both experiments, valuable items were more confidently recognized, further supporting that memory for valuable items is

improved. These findings suggest that value strengthens episodic encoding in older adults resulting in a greater reliance on recollection at test.

A major focus of both experiments was to examine how memory for associated incidental details was affected by item value. In Experiment 1, remembering was associated with increased point-value retrieval, regardless of age group. In contrast, a Value X Memory Type Interaction was observed such that remembered high-value items showed less associated color retrieval than high-value known items and low-value recollected items. Though a reduction of detail retrieval during recollection may seem counterintuitive, these findings are consistent with Hennessee et al. (2017), and the different pattern of results for these details may stem from how they related to the task. Point-values were highly relevant to the task, and this finding suggests that when an item is deeply encoded—as observed by later recollection—there is greater binding between the item and its value. In contrast, details irrelevant to the task, such as word color, may not be attended to and thus not strongly bound to the item. Put another way, deeply encoding valuable items may bind relevant incidental details at the expense of irrelevant details. Emotionally arousing images lead to enhanced binding of within-object features, such as color and spatial location, as this arousal provides the focused attention necessary for binding to occur (see Mather & Sutherland, 2011 for a review). The current findings suggest that binding of task-relevant details is prioritized over irrelevant details. In fact, these irrelevant details may be bound to valuable items less well. Although no significant age effects were observed, a post hoc analysis suggested that whereas younger adults predominantly retrieved high point-values through recollection, older adults showed more familiarity for this detail. There may be age-related differences in the capacity to bind relevant details to valuable items, though this finding requires support from additional research.

In Experiment 2, older adults had worse memory for associated item context, consistent with research showing decreased memory for source details (Koen & Yonelinas, 2014). Specifically, an Age X Value Interaction showed that only younger adults had enhanced retrieval of context for valuable items. The direction of this effect was supported by younger adults' similar retrieval rates for incongruent items and their baseline memory performance when value was not manipulated. The imagined context was arbitrarily associated with the valuable item, but in everyday life item location is arguably one of the most important details to remember. When hungry, knowing you have an energy bar is only valuable if you can remember where it located. Thus, the association of item to a spatial context may be more relevant for valuable items than the association with arbitrary perceptual details of the item. Furthermore, the imagined context in the present task could enrich semantic encoding of the item. Considering the sizable amount of information provided on study trials, it is likely that older adults selectively attended to items at the expense of encoding the context. Unlike in Experiment 1, the reduced encoding of contextual details for valuable items in older adults may not be advantageous.

These results demonstrate that associative binding at encoding is sensitive to the importance of the to-be remembered information. These findings suggest that there may be capacity limitations in binding such that strategically focusing on item information reduces memory for irrelevant details. Because this effect was accompanied by better recollection of valuable items, and was similar for older and younger adults, it may be that this increased focus on important items during encoding is preserved in healthy aging and may underlie the good VDR performance in older adults. However, the results of Experiment 2 suggest that an increased focus on important items during encoding by older adults may also lead to reduced memory for contextual information that could be relevant. Because there was no incentive for

selective encoding in Experiment 2, better learning of valuable items was unlikely intentionally strategic. Rather, the enhanced encoding of valuable items may have been relatively automatic. In older adults, resource limitations could lead to reduced encoding of contextual details when more attention is directed toward the important items. In younger adults, greater capacity could result in better binding of contextual details to important items. Our results suggest that aging may be accompanied by differences in the ability to encode contextual details, at least as measured by explicit memory for those details. Because older adults were sensitive to item value when presented at encoding, it was not the case that context memory deficits were entirely due to difficulty reinstating context at time of test. It would be interesting to see if older adults could demonstrate memory for contextual details using implicit measures, which would suggest that binding in explicit and implicit memory may be differentially affected in older adults.

The present results demonstrate that older adults selectively encode valuable items, leading to enhanced memory for these items. Furthermore, value increases recollection in older adults as much as in younger adults. Strongly encoding valuable items appears to promote binding of task-relevant details to items, though this may come at a cost to binding incidental perceptual and contextual details to the valuable item, particularly in older adults.

Chapter 3

Forget Me Not: Encoding Processes in Value-Directed Remembering

Joseph P. Hennessee, Alan D. Castel, & Barbara J. Knowlton

Valuable items are often remembered better than less valuable items, but research on the mechanisms supporting this value effect is limited. In the current study, we sought to determine how items might be differentially encoded based on their value. In Experiment 1, participants studied words associated with point-values which were followed by a cue to either "Remember" the word for a later test or "Forget" the word. While to-be-forgotten words were recognized at a lower rate than to-be-remembered words, there was a significant effect of value for to-be-forgotten words, even when the "Forget" cue was presented immediately after the word, suggested a relatively automatic enhancement of encoding by value. In contrast, older adults showed effects of value for to-be-remembered items only, suggesting that this automatic enhancement of encoding may be attenuated with age. In Experiment 2, we examined to what extent subjects engage in more effective encoding strategies for high-value items. Subjects studied a list of words with different point-values, and were instructed either to construct a mental image of the item, use rote rehearsal to learn the items, or were not given any study strategy. There were significant effects of value for items that were studied under rote rehearsal or when no strategy instruction was given. However, effects of value were nearly eliminated when subjects used a mental imagery strategy for all items as this strategy boosted memory for low-value items. Thus, it appears that subjects engage in more effective encoding strategies for

high-value words because the benefit of value was substantially reduced when an effective deep encoding strategy was used for all items. Together, these results suggest that valuable items are encoded more effectively due to both automatic and strategic mechanisms.

3.1 Introduction

When more information is present than can be remembered, learners typically selectively encode valuable items at the expense of less important ones (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Ariel, Price, and Hertzog, 2015). Selective encoding is used frequently in everyday life, such as attempting to remember one's grocery list or focusing on important information in a textbook chapter. In free recall and recognition testing, items are more likely to be remembered when paired with a high monetary-value or point-value at study (i.e., where goal is to earn a high score), and this value-related selectivity is preserved in healthy aging (Adcock et al., 2006; Castel, Murayama, Friedman, McGillivray, & Link, 2013; Cohen, Rissman, Suthana, Castel, & Knowlton, 2016; Mason, Farrell, Howard-Jones, & Ludwig, 2017; Shigemune, Tsukiura, Kambara, & Kawashima, 2014; Spaniol, Schain, & Bowen, 2013; Stefanidi, Ellis, & Brewer, 2018; Wolosin, Zeithamova, & Preston, 2012). This phenomenon has been labeled *value-directed remembering* (e.g., Castel et al., 2002). On one hand, people may be strategic and engage in deeper, more effective encoding of information they deem to be important to remember. For example, after a delicious meal one may try to "make a mental note" of the restaurant so it can be revisited. On the other hand, valuable information may be automatically strengthened in memory through effects of reward on memory representations. For example, a delicious meal may be remembered well because of the rewarding and pleasurable aspects of the experience even if no effort is made to encode the memory effectively. This more automatic effect of value is supported by a wide literature showing that valuable items are better

remembered even when encoding is incidental (Madan & Spetch, 2012; Mather & Schoeke, 2011; Murayama & Kitagami, 2014) or an implicit memory test is administered (Madan, Fujiwara, Gerson, & Caplan, 2012). These two mechanisms are not mutually exclusive, and it is possible that the two contribute differentially depending on the circumstances.

3.1.1 Potential Mechanisms Supporting Value-Directed Remembering. Research on explicit strategy use during the selective encoding of valuable material is somewhat limited. In Ariel, Price, and Hertzog (2015) both younger and older adults reported using more elaborative encoding strategies when learning high-value word pairs (i.e., mental imagery, putting items in a sentence), and using these strategies was associated with better recall than simple rote rehearsal. These elaborative strategies use deeper semantic and associative processing, which produces a stronger memory trace (Craik & Lockhart, 1972; Richardson, 1998). In Cohen, Rissman, Hovhannisyan, Castel, and Knowlton (2017), a large proportion of participants also reported using different mnemonic strategies based on item-value. Interestingly, many of these participants reported that they did not even attempt to selectively learn valuable items, but despite this supposed indifference to value, they still exhibited better memory for valuable material. This suggests that although learners often differentially employ mnemonic strategies based on item-value, some of the benefits of value are likely independent of strategy use.

Although it is possible value enhances memory primarily due to deeper, elaborative encoding, another possibility is that valuable items are selectively-attended, resulting in increased mental rehearsal. Indeed, when participants are given a limited time to study items differing in value, they will allocate a substantially disproportionate amount of time to studying the highest-value items (Ariel, Dunlosky, & Bailey, 2009; Ariel, Price, & Hertzog, 2015; Castel et al., 2013). This allocation of study-time coincides with enhanced retrieval of the valuable

items (Castel et al., 2013), and suggests that this value-related selective-attention is often intentional. According to the agenda-based regulation framework of study-time allocation, time, resources and effort are allocated based on a goal-oriented agenda that aims to maximize performance (Ariel, Dunlosky, & Bailey, 2009; Dunlosky & Ariel, 2011). Thus, if one can only remember a subset of the items being studied, the agenda will favor allocation of these things towards the most valuable items. In line with this framework, a commonly reported strategy is to ignore low-value items resulting in higher scores (Ariel, Price, & Hertzog, 2015; Robison & Unsworth, 2017). Additionally, valuable items may benefit from enhanced semantic processing. High-value cues have been shown to result in increased activity in ventrolateral prefrontal cortex (VLPFC), pre-supplementary motor area, and posterior lateral temporal cortex, for younger adults (Cohen, Rissman, Suthana, Castel, & Knowlton, 2014) and older adults (Cohen et al., 2016). These three regions have all been associated with deep semantic processing (Binder et al., 2009; Binder and Desai, 2011). In Cohen et al. (2016), younger adults who effectively increased activity in these regions for valuable items showed the strongest benefits of value, whereas older adults who decreased activity for low-value items performed best. It has not yet been determined whether such semantic processing differences are due to conscious strategy use.

Whereas the above literature suggests that value's effect on memory is supported by learners' intentional use of agenda-based encoding strategies and selective direction of attention, other researchers have focused on mechanisms that may support value's effect on memory in a relatively automatic fashion based on proximity to reward or value. Much of this work follows from studies of the mesolimbic reward system, suggesting that activity in these dopaminergic regions is increased for valuable items compared to less valuable items, which promotes the consolidation of memory for valuable items (Adcock et al., 2006; Carter, MacInnes, Huettel, &

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Adcock, 2009; Spaniol, Schain, & Bowen, 2013). More specifically, the nucleus accumbens and ventral tegmental area (VTA) are activated in response to high-value cues and this response is thought to underlie anticipation of large gains and losses (Carter et al., 2009). According to one popular hypothesis, dopaminergic signaling from the VTA in response to rewarding stimuli modulates hippocampal activity, and this signaling strongly influences whether new learning is persistently stored in long-term memory (Bethus, Tse, & Morris, 2010; Rossato, Bevilaqua, Izquierdo, Medina, & Cammarota, 2009; see Sugrue, Corrado, & Newsome, 2005 for a review).

  3.1.2 Overview of the Current Experiment. In the current study, we sought to determine the contributions of strategic and automatic encoding mechanisms in value-directed recognition. One method of examining the relative contribution of different encoding mechanisms was devised by Gardiner, Gawlik, and Richardson-Klavehn (1994), who used a directed-forgetting procedure with a cue to remember or forget the word presented either immediately or a few seconds after the word was presented. In this way, the effects of directed-forgetting could be measured, as well as the effects of elaborative encoding, which occurred when participants received a cue to remember immediately after the item was presented. When the cue was delayed, participants appeared to engage in maintenance rehearsal until the cue was presented, with little time for further elaborative rehearsal before the next item appeared. In Experiment 1 we used a similar directed-forgetting paradigm where each item was designated as to-be-remembered (TBR) or to-be-forgotten (TBF) after a variable delay during study, and then both TBR and TBF items were presented at test. The learn cue was either presented immediately after the word or after a 5 s delay, and value was manipulated by pairing each item with a point-value (3 or 12 pts.) that would be earned for later recognition. Delaying the cue leads participants to primarily keep an item in mind through maintenance rehearsal, as it is not in their interest to

expend cognitive resources elaborately encoding the item when a forget cue may appear (Gardiner, Gawlik, & Richardson-Klavehn, 1994; Woodward, Bjork, Jongeward, 1973). Thus, trials with a delayed cue encourage increased maintenance encoding at the expense of elaborative encoding. In contrast, an immediate "Remember" cue encourages elaborative encoding, as evidenced by improved recollection (Gardiner, Gawlik, and Richardson-Klavehn, 1994). Thus, if value's effect on recognition is primarily due to increased maintenance rehearsal, valuable items should be remembered relatively better when the directed-forgetting cue is delayed, whereas if participants engage in more elaborative encoding for high-value items, this effect should be greatest for items with an immediate Remember cue. Finally, if value's effect on recognition is largely automatic, this would be observable by value enhancing memory despite an immediate forget cue. Based on the findings of Ariel, Price, and Hertzog (2015) and Cohen et al. (2017), we hypothesized that value effects would be most pronounced on trials supporting elaborative encoding.

A striking finding in the cognitive aging literature is that value-directed remembering is well preserved in older adults (Ariel, Price, & Hertzog, 2015; Castel et al., 2002; Castel et al., 2011; Cohen et al., 2016; Spaniol, Schain, & Bowen, 2013). However, it is possible that older adults selectively encode valuable items in a manner differently than younger adults. Research suggests that value-related selectivity in older adults, but not younger adults, is associated with working memory capacity (Castel, Balota, & McCabe, 2009), raising that possibility that the effects of value are more related to strategic processes in older adults.

3.2 Experiment 1

3.3 Method

3.3.1 Participants. Data from 19 older adults (10 females and 9 males) from Los Angeles were collected for this study. Their age range was 61-87 years (M = 74.42, SD = 7.07). Participants were required to have no prior diagnosis of memory disorder (e.g., dementia) and they were in good health (M = 8.63, SD = 1.31) on a scale from 1 (poor health) to 10 (excellent health). The highest level of education achieved was graduate school (n = 8), college (n = 8), high school (n = 1), or other (n = 2). Participants were paid $10 per hour of participation.

Data from 34 undergraduate students from University of California, Los Angeles (UCLA) were collected as a cross-sectional comparison group. Two participants were excluded from all analyses for having recognition sensitivity (see Data Analysis section) more than 2.5 standard deviations below average, resulting in a total sample size of 32 (23 women and 9 men). Their age range was 18-38 (*M* = 21.50, *SD* = 3.46). This sample size was selected as it would allow for an approximate power of .81 to detect a medium-sized effect, as computed using GPower (version 3.0; Heinrich Heine Universität Düsseldorf; http://www.gpower. hhu.de /en.html). These participants completed the study for course credit. Informed consent was acquired and the study was completed in accordance with UCLA's Institutional Review Board.

3.3.2 Materials. Stimuli consisted of 96 six-letter English words, including nouns, adjectives, and verbs. These words were selected to have a similar frequency (M = 4466.12 occurrences per million, SD = 237.11) in the Hyperspace Analogue to Language corpus (Lund & Burgess, 1996). During encoding, 48 of these words were randomly presented and paired with a point-value of 3 or 12 presented to the right of the word (e.g., "rivers 3"). These values were chosen to maximize the difference between low (3 pts.) and high (12 pts.) value items while only

having two options for later source retrieval. Each word was printed in either red (RGB value: 255, 0, 0) or blue (RGB value: 0, 0, 255). Participants were not asked to memorize the point-value or word color; these details were used to assess incidental memory. Finally, each word was associated with either a learn ("LLLL") or forget ("FFFF") cue. Of the 48 study items, each possible point-value x word color x learn cue combination was assigned an equal number of trials, and all words were randomly assigned to each of these variable combinations or to be a new item at testing. During the recognition test all 96 words (half new) were presented in random order without a point-value and printed in black ink. All materials were designed and presented on a desktop computer using the Collector program (Gikeymarcia/Collector, n.d.; https://github.com/gikeymarcia/Collector). All words were printed in 29 pt. Open Sans font with a white background.

3.3.3 Procedure. Participants completed the study individually in a private computer lab. They were told they would view a large number of words, each paired with a point-value they would earn if they could remember the item, and that their goal was to maximize their score. They were told that items paired with a learn cue ("LLLL") were to be learned for a later memory test and items paired with a forget cue ("FFFF") could be forgotten. Each of the 48 study items were split into two cue delay blocks. In the short cue delay block, all items were presented individually for 2 s each, a learn/forget cue was presented for 1 s, and then there was a fixation cross for 5 s (Figure 3.1). In the long delay block, the order of the learn/forget cue and fixation cross were reversed, though the total duration of encoding was equal. Whether the long delay or short delay block was presented first was counterbalanced across participants. After encoding, a brief distractor task was completed to reduce additional rehearsal, which consisted of 10 simple multiplication and division problems.

Finally, a self-paced recognition test was completed. Participants were informed that they should disregard that some items were previously paired with a forget cue, as they would still earn their associated points. Additionally, to discourage them labeling all items as old, they were told they would lose 2 points for incorrect responses and to answer as accurately as possible. Participants first rated how confident they were that each item was or was not presented before on a 6-point scale: 1 "Definitely NEW", 2 "Probably NEW", 3 "Maybe NEW", 4 "Maybe OLD", 5 "Probably OLD", or 6 "Definitely OLD". For items rated as old (4-6), they then reported whether each item was worth 3 or 12 points and whether it was printed in red or blue ink. For items rated as new (1-3), they completed a filler question where they rated the pleasantness of the word.
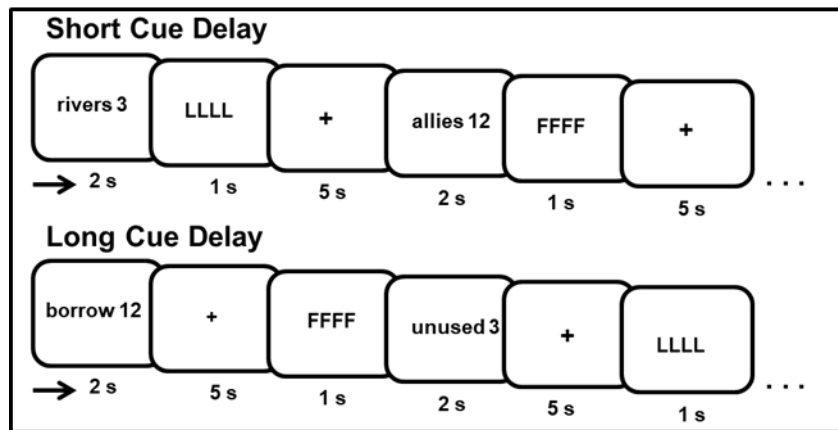
Figure 3.1. Encoding trial design for the short cue delay and long cue delay blocks for Experiment 1.

3.3.4 Data Analysis. Data were analyzed using SPSS (ver. 22) and ANOVAs were Greenhouse-Geisser corrected. Recognition performance was examined using the signal detection sensitivity measure A_z. Recognition sensitivity, A_z, measures one's ability to distinguish old items from new ones and ranges from 0 to 1 with chance performance at 0.5. Unlike most measures of recognition performance, this measure is largely unaffected by response bias and is computed as the area under the area under the hit rate by false alarm rate curve where each

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confidence response from highest to lowest confidence is treated as an "old" response (Stanislaw

& Todorov, 1999). Memory performance for incidental details (i.e., color and point-value) was

near chance, thus these data were excluded from analysis.

3.4 Results

3.4.1 Recognition Performance and Directed-Forgetting. Older adults displayed lower

recognition sensitivity, measured with A_z ($M = .73$, $SD = .10$), than younger adults ($M = .81$, SD

$= .07$), $t(49) = -3.09$, $p = .003$, $d = -0.87$. More specifically, older adults ($M = .57$, $SD = .18$) had

a lower hit rate than younger adults ($M = .72$, $SD = .13$), $t(49) = -3.39$, $p = .001$, $d = -0.95$,

though false alarm rates did not significantly differ between young ($M = .21$, $SD = .11$) and old

($M = .21$, $SD = .19$), $t(49) = 0.16$, $p = .692$, $d = 0.04$. Across age groups, a robust main effect of

cue was observed, $F(1,49) = 54.50$, $p < .001$, $\eta_p^2 = .53$, such that TBR items ($M = .78$, $SD = .09$)

were recognized with higher sensitivity than TBF items ($M = .71$, $SD = .08$). Thus, the cue was

effective in modifying encoding across groups. The Age x Cue interaction displayed a trend,

$F(1,49) = 3.53$, $p = .066$, $\eta_p^2 = .07$, for the directed-forgetting effect (TBR – TBF) to be larger for

younger adults ($M = .11$, $SD = .06$) than older adults ($M = .06$, $SD = .09$), $t(49) = 2.28$, $p = .027$,

$d = 0.64$. The value effect on sensitivity was smaller and not significant when averaged across all

directed-forgetting conditions, $F(1,49) = 1.13$, $p = .294$, $\eta_p^2 = .02$, and the Value x Age

interaction was not significant, $F(1,49) = 0.20$, $p = .657$, $\eta_p^2 < .01$. However, for younger adults,

item-value was effective in modifying encoding, as high-value TBR items ($M = .83$, $SD = .08$)

were recognized with higher sensitivity than low-value TBR items ($M = .81$, $SD = .07$), $F(1,31)$

$= 4.78$, $p = .037$, $\eta_p^2 = .13$.

3.4.2 Effects of Elaborative Encoding. To determine the extent that elaborative encoding

contributed to value-directed remembering, we next examined the effects of Cue and Delay for

high-value and low-value items (Figure 3.2). For valuable items, the Age x Cue x Delay interaction was not significant, $F(1,49) = 2.21$, $p = .144$, $\eta_p^2 = .04$, nor were any other interactions with Age (all p's > .102). Most importantly, the Cue x Delay interaction was not significant, $F(1,49) = 1.34$, $p = .252$, $\eta_p^2 = .03$, though a substantial main effect of Cue was observed, $F(1,49) = 28.92$, $p < .001$, $\eta_p^2 = .37$, such that TBR items were better remembered than TBF items. Sensitivity did not significantly differ between valuable TBR items paired with an immediate or delayed learn cue, $t(50) = 0.95$, $p = .346$, $d = 0.14$. These results indicate that both age groups better remembered valuable items associated with a learn cue, but that having that cue immediately after learning, thus allowing for the maximum amount of elaborative encoding, did not significantly affect later retrieval.

When examining low-value items, the Age x Cue x Delay interaction again was not significant, $F(1,49) = 1.72$, $p = .681$, $\eta_p^2 < .01$, nor were there any other significant interactions with age (all p's > .113). A significant main effect of Cue was again observed, $F(1,49) = 37.48$, $p < .001$, $\eta_p^2 = .43$, such that TBR items were better remembered than TBF items. Although a significant Cue x Delay interaction was observed, $F(1,49) = 9.20$, $p = .004$, $\eta_p^2 = .16$, this was largely due to performance differences for TBF items as no significant difference was observed between low-value items given an immediate or delayed learn cue, $t(50) = 1.69$, $p = .098$, $d = 0.24$.
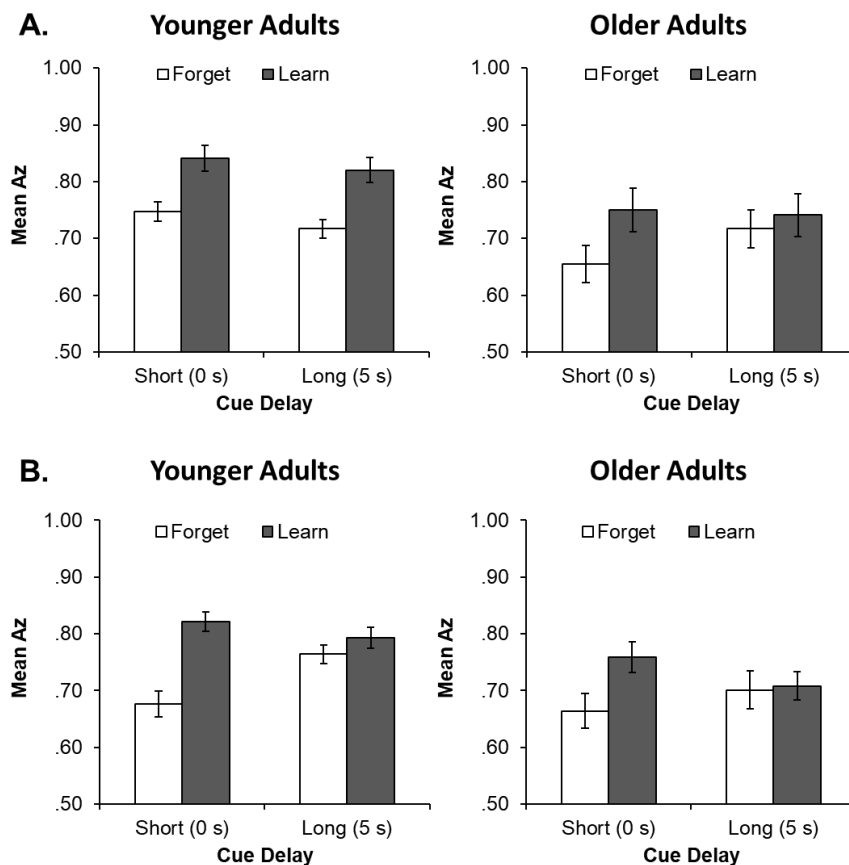
Figure 3.2. Recognition sensitivity (A$_z$) by cue and cue delay in Experiment 1 for: **A)** High-value items. **B)** Low-value items. Error bars represent one standard error from the mean.

3.4.3 Effects of Maintenance Rehearsal. Contributions of maintenance rehearsal were examined by examining the effects of cue delay for TBF and TBR items separately (Figure 3.3). For TBF items, an Age x Delay x Value interaction was observed, $F(1,49) = 4.24$, $p = .045$, $\eta_p^2 = .08$, so results of each group were examined individually. Younger adults showed a significant Delay x Value interaction, $F(1,49) = 8.25$, $p = .007$, $\eta_p^2 = .21$. Specifically, low-value TBF items were recognized significantly better when the cue was delayed, $t(31) = 3.20$, $p = .003$, $d = 0.57$, though this delay did not significantly affect memory for valuable TBF items, $t(31) = 1.07$, $p = .295$, $d = 0.19$. These results indicate that increasing a period of maintenance rehearsal benefitted low value TBF items. For high value items, delaying the "Forget" cue did not further increase

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recognition. In contrast, older adults only showed a weak trend for a main effect of Delay, $F(1,18) = 3.44$, $p = .080$, $\eta_p^2 = .16$ and with neither high-value nor low-value items showing a significant delay effect (all p's $> .089$).

Next, TBR items were examined. The Age x Delay x Value interaction was not significant, $F(1,49) = 0.41$, $p = .525$, $\eta_p^2 = .01$, nor were any other interactions with Age (all p's $> .672$). Only a weak trend for Delay was observed, $F(1,49) = 3.13$, $p = .083$, $\eta_p^2 < .01$, such that performance was numerically higher when the learn cue was immediate ($M = .79$, $SD = .09$) as opposed to delayed ($M = .77$, $SD = .11$). In summary, increasing maintenance rehearsal by delaying the cue was only found to be beneficial for younger adults studying low-value TBF items.

3.4.4 Automatic Effects of Value on Memory. Relatively automatic contributions to value-directed remembering were examined by looking at performance for items paired with an immediate forget cue (Figure 3.3 Panel A). As mentioned previously, the Age x Delay x Value interaction was significant, so both groups were examined separately. For younger adults, greater recognition sensitivity was observed for high-value items than low-value items followed by an immediate "Forget" cue, $t(31) = 2.87$, $p = .007$, $d = 0.51$. Note that both high-value items, $t(31) = 14.38$, $p < .001$, $d = 2.54$ and low-value items, $t(31) = 7.78$, $p < .001$, $d = 1.38$ were recognized with better than chance performance. For older adults, this effect of value for items paired with an immediate forget cue was not observed, $t(18) = 0.23$, $p = .822$, $d = 0.05$. For older adults, both high-value items, $t(18) = 4.64$, $p < .001$, $d = 1.06$ and low-value items, $t(31) = 5.25$, $p < .001$, $d = 1.21$ were recognized with better than chance performance.
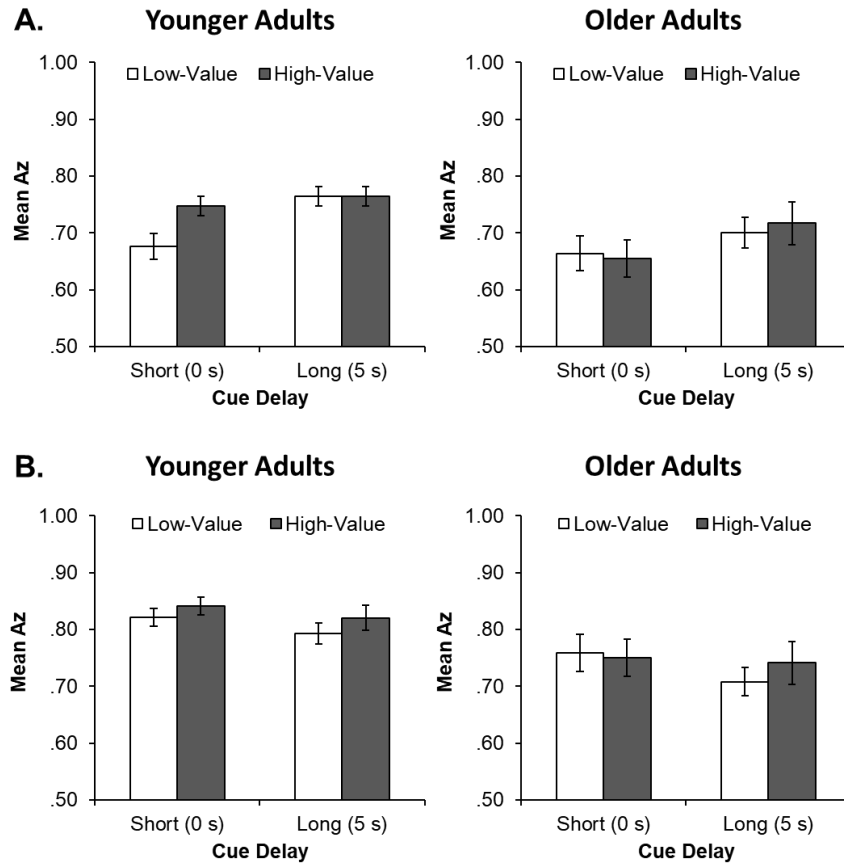
Figure 3.3. Recognition sensitivity (A_z) by value and cue delay in Experiment 1 for: **A)** To-be-forgotten items. **B)** To-be-remembered items. Data re-plotted from Figure 3.2 for illustrative purposes. Error bars represent one standard error from the mean.

3.5 Discussion

Both age groups showed strong directed-forgetting, suggesting that this manipulation was effective in altering encoding. Perhaps most importantly, we observed in younger adults a strong value-directed remembering effect for items paired with an immediate forget cue. As deliberate encoding is substantially reduced with an immediate forget cue (Bjork, 1989; Wylie, Fox, & Taylor, 2007), this suggests that a relatively automatic process is contributing to value's effect on memory. Interestingly, this relatively automatic value effect on recognition was not observed in older adults, as their sensitivities for high- and low-value items with an immediate forget cue did

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not significantly differ. This age difference was supported by a significant Age x Delay x Value interaction. One candidate mechanism to explain this difference is that it was mediated by age-related differences in the dopaminergic system (Mukherjee et al., 2002). If valuable items produce an increase in activity in reward-related dopaminergic systems, and this increase enhances encoding of these items, reductions in this effect with aging may lead to reduced automatic effects of value on memory. Prior work in healthy young subject has shown enhanced memory for items presented in temporal proximity to rewards (Murayama & Kitagami, 2014), consistent with the idea that the presentation of unexpected reward increases dopamine release in hippocampus, enhancing encoding of proximal material. In a neuroimaging study of value-directed remembering, older adults were shown to have reduced activity in midbrain dopaminergic regions in response to the value cue (Cohen et al., 2016) consistent with a reduced role of this system in value effects on memory in aging.

Contrary to our predictions, we did not observe a significant increase in recognition sensitivity when participants were given an immediate cue to remember the word, thus prolonging the period for elaborative encoding. Although TBR items were much more likely to be remembered than TBF items, performance did not significantly differ whether the cue came immediately after the word or after a 5 s delay. When the cue was presented after the delay, there was only 1 s until the next word appeared. It seems unlikely that 1 s of encoding was enough to fully use more complex elaborative strategies such as mental imagery or putting items into a sentence, particularly for older adults. Although studies involving multiple study-test lists with feedback find that older and younger adult participants selectively apply elaborative strategies based on item-value (Ariel, Price, & Hertzog, 2015; Cohen et al., 2017) it may be that such differences in elaboration are less pronounced when learning a single list without intermittent

feedback. This feedback may help them develop more selective encoding strategies (Cohen et al., 2017). Thus, participants may have engaged primarily in maintenance rehearsal in all conditions except the immediate forget condition. In younger adults, it may have been possible to engage in additional effective encoding in the delayed TBR condition, as that condition led to superior recognition sensitivity than the delayed TBF condition. The 1 s of encoding time after the delayed Remember cue did not appear to benefit older adults, as their performance was similar for delayed cue conditions.

Older adults generally show reduced directed-forgetting due to difficulty in the attentional inhibition of items (Hogge, Adam, & Collette, 2008; Zacks, Radvansky, & Hasher, 1996). For low value items in the present study, older adults did show an attenuated directed forgetting effect when the Forget cue was presented immediately. However, the directed forgetting effect was significantly lower in young adults for valuable items compared to low-value items. In contrast, value did not reduce directed forgetting in older adults, indicating that only younger adults were relatively less able to forget high value items.

3.6 Experiment 2

In Experiment 1, at least for younger adults, we found evidence of relatively automatic enhancement of encoding of high-value words, in that these words were recognized better than low-value words after an immediate "Forget" cue. Effects of value were not significant for conditions in which participants were instructed to remember items, suggesting that value did not affect encoding strategies. However, a limitation of Experiment 1 was that the directed-forgetting manipulation may have discouraged participants from differentially engaging in effortful encoding strategies. Participants may have focused attention on whether or not the items were TBR or TBF and they may have found it too demanding to also vary encoding strategy by value.

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In order to assess whether participants are able to engage in elaborative encoding of high-value items, in Experiment 2 we removed the directed-forgetting manipulation and instead simply instructed participants to learn using different encoding strategies. In three between-subjects groups, participants were either given no instruction regarding what strategy to use or they were instructed to use a mental rehearsal strategy or a mental imagery strategy for all learned items. After recognition testing, participants reported whether they adhered to their assigned strategy. We hypothesized that if differences in recognition accuracy between high- and low-value items were due to in part to differences in the depth of encoding, instructing participants to encode all learned items with an elaborative mental imagery strategy would mitigate these differences. Our previous work has shown that high-value items are more likely to be recollected at test (Hennessee, Castel, & Knowlton, 2017; Hennessee, Knowlton, & Castel, 2018). Thus, if participants were achieving superior recollection of high-value items because of differential use of elaborate encoding strategies, we predicted that instructing participants to use a mental imagery strategy for low-value items would reduce this difference in recollection. Alternatively, if the effects of value are restricted to automatic strengthening of memory representations, there may continue to be a difference between high-value and low-value items, even though overall recognition may be better when this elaborative encoding task is used. To assess recollection, we used a Remember-Know-Guess design where participants introspected whether each item they each item they classified as "old" was accompanied by recollection of the study episode including associated details (Remember response), a strong sense of familiarity (Know response), or whether their recognition response was a guess (Gardiner & Ramponi, 1998; Tulving, 1985). We also assessed memory for the highest confidence responses ('Definitely Old') as there are appreciable differences between confidence and recollection (Gardiner & Java,

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1990) that may lead these responses to be differentially affected by encoding strategy. In this way, we were able to assess whether value affected the quality of recognition and how this compared with the effect of encoding instruction.

3.7 Method

3.7.1 Participants. Data from 108 UCLA undergraduate students were collected for this experiment. Participants in the rehearsal and imagery conditions who reported using the pertinent strategy less than 50% of the time were excluded from all analyses, leaving 36 participants in the No Instruction condition, 20 participants in the Mental Rehearsal condition, and 24 participants in the Mental Imagery condition. This final sample of 80 students (59 females and 21 males) had an age range of 18-27 years ($M = 20.20$, $SD = 1.64$). This sample size was selected as it would allow for an approximate power of .85 to detect a medium-sized instruction condition by value interaction, as computed using GPower. These participants completed the study for course credit. Informed consent was acquired and the study was completed in accordance with UCLA's Institutional Review Board.

3.7.2 Materials. Stimuli included 96 English nouns, and the first letter of each word was capitalized. All words were drawn from clusters 7 and 8 of the Toglia and Battig (1978) word norms, as these clusters were high in imagability. Words were selected to have similar imagability ($M = 5.66$, $SD = 0.40$, range: 4.75-6.61), concreteness ($M = 5.75$, $SD = 0.37$, range: 4.50-6.48), and number of letters ($M = 5.78$, $SD = 0.73$, range: 5-7). During encoding, 48 of these words were randomly presented and paired with a point-value of 1, 2, 3, 10, 11, or 12 to the right of the word. These values were chosen to maintain a large difference between low-value (1-3 pts.) and high-value (10-12pts.) items and yet to provide a larger range of values than Experiment 1. This wider selection of point-values was also used to make the work more

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comparable to recent examinations of value and memory (Cohen et al., 2016; Hennessee, Knowlton, & Castel). Whether an item was assigned to be low-value, high-value, or a new item at test was counterbalanced across participants. During the recognition test all 96 words (half new) were presented in random order in black on a white background screen without a point-value. All materials were presented on a desktop computer with the E-prime 2.0 software (Psychology Software Tools Inc., Pittsburgh, PA; https://www.psnet.com). All words were presented in 32 pt. Arial font.

3.7.3 Procedure. Participants completed the study individually in a private computer lab. They were told they would view a large selection of words, each paired with a point-value they would earn if they could remember the item, and that their goal was to earn a high score. Instructions regarding how they should learn items were varied between-subjects. The No Instruction condition was not provided instruction as to which strategy to use, the Mental Rehearsal condition was instructed to think of the word repeatedly (e.g., "Knight, Knight, Knight, . . ."), and the Mental Imagery condition was asked to picture in mind what the item looks like. During the encoding phase, participants were presented with 48 words that were each on screen for 2 s and with a 1 s fixation cross between words. After encoding, participants completed seven multiplication and division problems as a distractor task. Afterwards, they were instructed regarding the meaning of Remembering, Knowing, and Guessing with instructions adapted from Gardiner and Java (1990; see Appendix). Participants were asked to explain what Remembering meant in the context of this study, and corrected if their response was deemed unsatisfactory.

Finally, participants completed a self-paced recognition test including 96 words (half new). Participants were told they would lose 2 points for incorrect responses to discourage

labeling all items as old. Participants first rated how confident they were that each item was presented before on the 6-point scale describe in Experiment 1 (1 "Definitely New" to 6 "Definitely Old"). For items rated as old (4-6), they reported whether they recognized the item due to Remembering, Knowing, or Guessing. For items rated as new (1-3), they completed a filler question where they rated the pleasantness of the word. This filler question was added to prevent participants from rating items as new to reduce the duration of the experiment. At the end, participants were asked to rate the proportion of time (0-100% in 10-percent increments) they used the following strategies: (a) mental imagery, (b) mental rehearsal, (c), putting items into a sentence. These strategies were targeted because Ariel, Price, and Hertzog (2015) found that they were commonly used.

3.8 Results

3.8.1 Strategy Use. First, the reported proportion of time participants used each strategy was examined to determine how well they followed instructions (Figure 3.4). The relationship between the encoding condition and use of the three strategies was examined using a 3 x 3 repeated measures ANOVA. A significant Condition x Strategy interaction was observed, $F(4, 145) = 6.86$, $p < .001$, $\eta_p^2 = .15$. In the Rehearsal Condition, using rehearsal was significantly more common than the other two strategies (all p's $\leq .002$). Likewise, in the Mental Imagery condition, using imagery was significantly more common than the other two strategies (all p's $\leq .005$). Finally, the No Instruction condition was examined to better understand normal strategy use on this value-directed remembering task. In this condition, rehearsal was the most common strategy (all p's $\leq .034$), though mental imagery was also quite common and was used more frequently than putting items into a sentence, $t(34) = 3.03$, $p = .005$, $d = 0.51$.
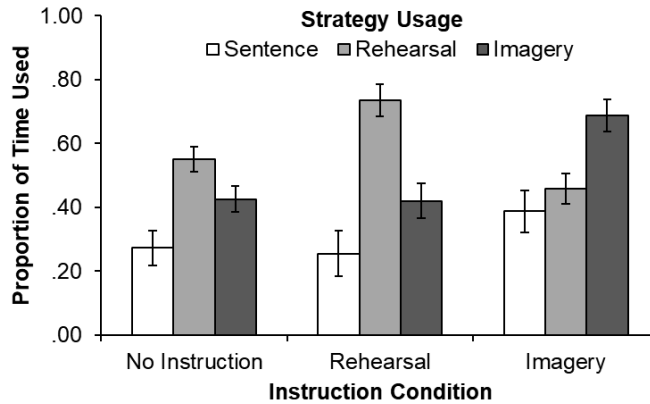
Figure 3.4. Self-reported proportion of time spent using each strategy for each of the instruction conditions in Experiment 2. Error bars represent one standard error from the mean.

3.8.2 Memory Performance. The influences of encoding condition and item-value on recognition sensitivity (A_z) were examined using a 3 x 2 repeated measures ANOVA (Figure 3.5; Table 3.1). The Condition x Value interaction only showed a trend, $F(2, 77) = 2.54$, $p = .085$, $\eta_p^2 = .06$. However, a follow-up ANOVA comparing sensitivity between the No Instruction and Mental Imagery condition did show a significant Condition x Value interaction, $F(1, 58) = 4.41$, $p = .040$, $\eta_p^2 = .07$. In the No Instruction condition, sensitivity was considerably higher for high-value items than low-value items, $t(35) = 4.38$, $p < .001$, $d = 0.74$. In the Rehearsal condition, sensitivity was also significantly higher for high-value items than low-value items, $t(19) = 3.61$, $p = .002$, $d = 0.82$. In the Mental Imagery condition, the value effect on sensitivity was smaller though still significant, $t(23) = 2.11$, $p = .046$, $d = 0.47$. Differences in sensitivity by value were considerably reduced in the Mental Imagery condition largely because although the sensitivity to low-value items significantly improved compared with the No Instruction condition, $t(58) = 3.43$, $p = .001$, $d = 0.91$, high-value items only showed a trend for improvement, $t(58) = 1.93$, $p = .058$, $d = 0.51$.

We then examined influences of encoding condition and item-value on the proportion of items given the highest confidence response ('Definitely Old'). The 3 x 2 repeated measures ANOVA showed a significant interaction of value and condition, $F(2, 77) = 4.31$, $p = .017$, $\eta_p^2 = .10$. In the No Instruction condition, 'Definitely Old' responses were given to a significantly higher proportion of high-value items ($M = .54$, $SD = .21$) than low-value items ($M = .34$, $SD = .20$), $t(35) = 5.17$, $p < .001$, $d = 0.86$. Likewise, in the Rehearsal condition, 'Definitely Old' responses were more common for high-value items ($M = .55$, $SD = .23$) than low-value items ($M = .34$, $SD = .17$), $t(19) = 3.72$, $p = .001$, $d = 0.84$. However, in the Mental Imagery condition, the proportion of items given a 'Definitely Old' response did not significantly differ between high-value ($M = .67$, $SD = .20$) and low-value items ($M = .62$, $SD = .19$), $t(23) = 1.47$, $p = .156$, $d = 0.30$. Unlike recognition sensitivity, the highest confidence responses increased in frequency in the imagery condition both for low-value items $t(58) = 5.53$, $p < .001$, $d = 1.46$, and valuable items, $t(58) = 2.43$, $p = .018$, $d = 0.65$.
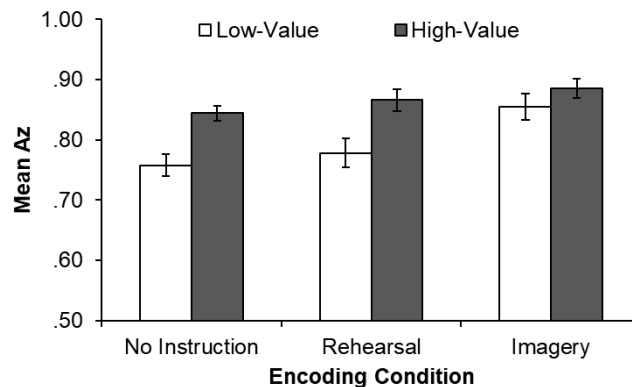

Figure 3.5. Recognition sensitivity (Az) by item-value and instruction condition in Experiment 2. Error bars represent one standard error from the mean.

Table 3.1. Experiment 2 Memory Performance and R-K-G experiences by Encoding Condition

	No Instruction		Rehearsal		Imagery	
	Low-Value	High-Value	Low-Value	High-Value	Low-Value	High-Value
Hit rate	.65 (.23)	.79 (.15)	.61 (.15)	.80 (.12)	.81 (.15)	.83 (.15)
False alarms	.26 (.15)	.26 (.15)	.20 (.14)	.20 (.14)	.19 (.16)	.19 (.16)
Confidence	4.22 (0.79)	4.85 (0.62)	4.15 (0.53)	4.88 (0.60)	4.92 (0.74)	5.09 (0.73)
R	.37 (.23)	.52 (.24)	.44 (.20)	.56 (.30)	.70 (.21)	.73 (.19)
K	.34 (.23)	.29 (.19)	.33 (.22)	.26 (.21)	.16 (.12)	.18 (.15)
G	.29 (.20)	.19 (.13)	.24 (.17)	.17 (.13)	.14 (.15)	.09 (.10)

Note. Standard deviations presented in parentheses. R = proportion Remembered, K = proportion Known, G = proportion Guessed.

3.8.3 Experiences of Remembering, Knowing, and Guessing. To examine whether the proportion of correctly recognized old items given a Remember, Know, or Guess response differed as a function of item-value and encoding condition (Table 3.1), a 3 x 2 x 3 repeated measures ANOVA was computed. The Memory type (R-K-G) x Condition x Value interaction was not found to be significant, $F(2, 77) = 1.54$, $p = .221$, $\eta_p^2 = .04$. A significant Memory type x Condition interaction was observed, $F(2, 77) = 11.01$, $p < .001$, $\eta_p^2 = .22$. Additionally, a significant Memory Type x Value interaction was observed, $F(1, 77) = 7.32$, $p = .008$, $\eta_p^2 = .09$. Posthoc analyses revealed that valuable items were more likely than low-value items to receive a Remember response at test, $t(79) = 3.85$, $p < .001$, $d = 0.43$, and less likely to receive a Guess response, $t(79) = -3.92$, $p < .001$, $d = -0.46$. The proportion of recognized items that received a Know response did not significantly differ by value, $t(79) = 1.31$, $p = .193$, $d = 0.15$.

Next, we examined how the proportion of items given a Remember response in the Mental Imagery condition compared with the No Instruction condition. We observed a significant Value x Condition interaction, $F(1, 58) = 4.15$, $p = .046$, $\eta_p^2 = .07$. More specifically, in the No Instruction condition, recognized high-value items were more likely to receive a Remember response than low-value items, $t(35) = 3.71$, $p = .001$, $d = 0.62$. But, the frequency of

Remember responses did not significantly differ by value in the Mental Imagery condition, $t(23)$ = 0.74, p = .467, d = 0.15. Interestingly, the Mental Imagery condition showed higher rates of remembering than the No Instruction condition both for high-value items, $t(58)$ = 3.52, p = .001, d = 0.96 and low-value items, $t(58)$ = 5.53, $p < .001$, d = 1.47.
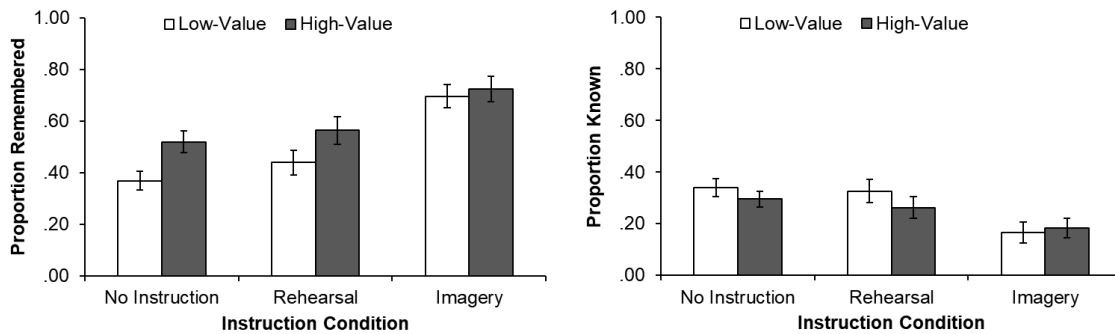
Figure 3.6. Proportion of items given a Remember (left) and Know (right) response by item-value and instruction condition. Error bars represent one standard error from the mean.

3.9 Discussion

A key finding was that instructing participants to learn all items using mental imagery mitigated value's enhancement of recognition. In contrast, valuable items were recognized and recollected at significantly higher levels than less valuable words when participants primarily used a less effective mental rehearsal strategy. Value-based differences in recognition sensitivity were substantially reduced in the Mental Imagery condition, and the frequency of highest confidence responses and recollection did not differ significantly by item-value because performance was sharply enhanced for low-value items. These results support the idea that participants are engaging in more elaborative encoding of high-value words, as the value effect was nearly eliminated when participants were instructed to engage in elaborative encoding of low-value words as well. In the other conditions, subjects reported primarily using a less effective rehearsal strategy, and recognition was significantly better for high-value words. It may

be that in these conditions, an automatic enhancement of encoding occurred for high-value words. However, it is also possible that participants did engage in some elaborative encoding for high-value words, as they reported using deeper encoding strategies for a substantial part of time. This interpretation is consistent with our prior neuroimaging work showing that participants with high value-related selectivity in memory show increased activity in left hemisphere semantic processing regions when encoding valuable items (Cohen et al., 2014).

3.10 General Discussion

3.10.1 Relatively Automatic Contributions to Value-Directed Remembering. Across two experiments, the contributions of relatively automatic and elaborative encoding processes to value–directed remembering were examined. A key result of this study was that value can enhance recognition in a relatively automatic fashion, even when subjects are immediately told that the item is irrelevant. In Experiment 1, when items were paired with an immediate forget cue, younger adults showed much stronger recognition sensitivity for valuable items than low-value items. The large directed-forgetting effect observed in this study suggests that an immediate forget cue effectively reduced intentional encoding of items; thus, the most plausible explanation for these results is that a less deliberate and relatively automatic process is enhancing the learning of valuable items. Interestingly, while older adults showed a directed-forgetting effect, there was no apparent effect of value for those items that they were immediately directed to forget. These results suggest an age difference in the mechanism by which value enhances subsequent memory.

One plausible mechanism by which valuable items may be automatically strengthened in memory is that these items activate midbrain dopaminergic circuitry that can enhance hippocampal activity (Bethus, Tse, & Morris, 2010; Rossato et al., 2009). High-value cues elicit

activity in dopaminergic regions and this dopamine release appears to signal the anticipation of rewards (Adcock et al., 2006; Carter et al., 2009). Furthermore, this dopaminergic signaling has been shown to act directly on the hippocampus to upregulate the storage of information in long-term memory (Lisman & Grace, 2005; Otmakhova, Duzel, Deutsch, & Lisman, 2013; Rossato et al., 2009). Neuroimaging of value-directed remembering has revealed that activation of bilateral nucleus accumbens, a component of the midbrain dopaminergic reward system, does coincide with high point-value cues (Cohen et al., 2014). In a previous study, the presentation of rewards strengthened subsequent memory for information that was proximal to these rewards, consistent with the idea that value can automatically enhance memory independent of motivation to remember (Murayama & Kitagami, 2014). In a similar vein, Cohen et al. (2017) showed that effects of value were present on a free recall task, even when subjects reported that they did not attend to value and attempted to encode all items in a similar fashion.

One difference between the current study and much of previous work showing activation of the midbrain dopamine system is that these previous effects were mainly apparent after a delay of at least 12 hours, suggesting that the effect of dopamine is to enhance memory consolidation (Bethus, Tse, & Morris, 2010; Rossato et al., 2009; Spaniol, Schain, & Bowen, 2013). In the present study, small effects of value were seen on a recognition test that occurred shortly after study, and these immediate effects of value have been observed in previous research (Hennessee, Castel, & Knowlton, 2017; Hennessee, Knowlton, & Castel, 2018). It may be that there would be larger value effects with a long delay due to enhanced consolidation of these items.

Interestingly, older adults in Experiment 1 did not show an automatic benefit of value on memory. When given an immediate forget cue, their recognition sensitivity for both low-value

and high-value items did not significantly differ. If the relatively automatic effect of value is driven by a dopamine-mediated effect, the fact that dopamine levels decline in normal aging (Mukherjee et al., 2002) may explain this pattern of results. Additionally, older adults show reduced activity in the dopamingeric NAcc and prefrontal regions in response to high-value cues (Cohen et al., 2016). While a large body of research has shown that older adults exhibit robust value-directed remembering effects, the present results suggest that there may be some age-related differences in the mechanism of the effects of value on memory.

3.10.2 Contributions of Elaborative Encoding. Other work has suggested that high-value cues promoted increased elaborative semantic processing of items which leads to better subsequent memory. Research by Cohen et al. (2016) suggests that value-directed remembering promotes increased activity in left VLPFC, pre-supplementary motor area, and posterior lateral temporal cortex, and these regions have been implicated in deep semantic processing (Binder et al., 2009; Binder and Desai, 2011). In Experiment 1, we did not observe a significant effect of prolonged elaborative encoding on recognition in either age group for high or low value words. More specifically, when the learn cue was presented immediately, participants had the maximal amount of time (6 s) to use any encoding strategy they preferred, but this was not shown to improve performance relative to seeing the cue only 1 s before the next item. At first glance, this seems at odds with prior research showing that both age groups selectively use effective strategies for valuable word-pairs (Ariel, Price, & Hertzog, 2015) and that younger adults alter their strategy use based on item-value (Cohen et al., 2017). Likewise, this seems to go against the agenda-based regulation model (Ariel, Dunlosky, & Bailey, 2009), as the longer study time should allow for larger differences in allocating time, resources, and effort based on item-value. However, as shown in Cohen et al. (2017), participants often require multiple study-test lists

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with feedback on their performance to fully develop this value-related selectivity in encoding. Ariel, Price, and Hertzog (2015) and Cohen et al. (2017) used multiple lists with feedback, whereas the present study did not. Thus it is possible that our participants did not have sufficient feedback on performance to develop selective encoding strategies observed in studies with multiple study-test lists. The contribution of elaborative encoding strategies on value-directed remembering may be relatively small when studying a single recognition list without intermittent feedback.

Nevertheless, in Experiment 2, there was evidence of differential encoding strategies for valuable items. Unlike in Experiment 1, participants in Experiment 2 did not have to engage in directed-forgetting, and thus it may have been easier to adopt different encoding strategies depending on value. A strong value effect on recognition was observed in the maintenance rehearsal condition, and this value effect was not significantly different than when no instruction was present. In these conditions, valuable items may have been automatically encoded more effectively, or participants may have strategically engaged in more effective encoding of these items. Even when participants were instructed to engage in rehearsal, it is possible that they were able to also engage in more semantic encoding of some items, as participants generally reported using more than one strategy during the encoding session. In support of the idea that participants engage in more semantic encoding strategies for high-value items, instructing participants to encode all learned items using a mental imagery strategy improved memory for low-value items to the point that value-based differences in sensitivity were reduced and differences in the rates of highest confidence response and Remember responses were eliminated. In a recent study, item-value was associated with increased experiences of recollection but the frequency of high confidence responses was not significantly affected by value (Hennessee, Castel, & Knowlton,

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2017); the current findings suggest that value can alter the frequency of these high confidence responses and that mental imagery may affect feelings of strong confidence and recollection similarly. The advantage for high-value items was essentially eliminated when participants engaged more generally in a semantic encoding strategy. In Cohen et al. (2016), neuroimaging data indicated differences in activation in semantic processing regions between high-value and low-value items, and we observed that differences in performance were mitigated when participants increase their semantic processing of low-value items through mental imagery. This differential activation in semantic processing regions was also present in older adults, suggesting that strategic encoding of high value items is preserved across the lifespan. Taken together, these two studies suggest that differences in semantic processing based on item-value contribute to value-directed remembering, though this contribution is likely greater when participants receive feedback through multiple lists.

3.10.3 Conclusions. Across two experiments we demonstrated that value can improves recognition in both a relatively automatic fashion as well as by inducing participants to engage in more effective encoding. Interestingly, the automatic process appeared not to contribute much to older adults' value-related selectivity. Further research may determine how older and younger adults adjust and apply encoding strategies to maximize memory efficiency.

Chapter 4

White Matter Integrity in Brain Structures Supporting Semantic Processing is Associated with Value-Directed Remembering in Older Adults

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In Preparation for Submission

White matter microstructure changes substantially in aging. To better understand how the integrity of white matter structures supports the selective learning of rewarding material, 23 healthy older adults were tested on a value-directed remembering task. This task involved successive free recall word lists where items differed in importance, as denoted by value cues preceding each word. White matter structure was measured using diffusion tensor imaging (DTI). We found that greater structural integrity (as measured by lower mean diffusivity) in bilateral inferior fronto-occipital fasciculus (IFOF) was associated with greater recall for high-value items, but not low-value items. Older adults with greater structural integrity in a tract involved in semantic processing are thus able to more successfully encode high-value items for subsequent recall. In contrast with similar investigations in younger adults, neither structural integrity of the uncinate fasciculus, nor the strength of anatomical connectedness between the bilateral nucleus accumbens to ventral tegmental area reward pathway, were correlated with memory for high-value items. These age differences likely result from older adults relying more on value-related modulation of semantic encoding strategies, and less on the engagement of reward circuitry, to selectively encode valuable information.

4.1 Introduction

Throughout life we are presented with more information than we can remember. In order to be efficient learners, we must selectively encode what is most valuable. One way to examine the degree to which an individual is engaged in selective learning is through the value-directed remembering (VDR) paradigm. In this task, items are paired with point-values that are earned with later retrieval, and the subject's goal is to earn a high score (Castel, Benjamin, Craik, & Watkins, 2002). A wide literature shows that the encoding and retrieval of various stimuli is enhanced when items are paired with a high point-value or monetary value (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Ariel, Price, & Hertzog, 2015; Carter, 2009; Cohen, Rissman, Suthana, Castel, & Knowlton, 2014), and that this value-related selectivity is often intact in normal healthy aging (Castel, Balota, & McCabe, 2009; Castel et al., 2002; Cohen, Rissman, Suthana, Castel, & Knowlton, 2016; Spaniol, Schain, & Bowen, 2014); see Geddes, Mattfield, de los Angeles, Keshavan, & Gabrieli, 2018, for a counterexample).

Multiple cognitive and neural mechanisms are theorized to underlie the strengthening of memories for high-value items. For one, value cues have been shown to elicit activation in a reward circuit, including the nucleus accumbens (NAcc) and ventral tegmental area (VTA), that is thought to represent anticipation of future rewards and that may influence goal-directed motivation (Adcock et al., 2006; Carter et al., 2009; Cohen et al., 2014). The VTA modulates long-term potentiation in the hippocampus through its dopaminergic connections (Bethus, Tse, & Morris, 2010; Rossato, Bevilaqua, Izquierdo, Medina, & Cammarota, 2009), and the NAcc, VTA, prefrontal cortex (PFC), hippocampus, and subiculum are theorized to form a loop that regulates goal-directed learning (see Lisman & Grace, 2005 for a review). However, some research has failed to find an increase in activity in reward-related regions for older adults during

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encoding of high-value items (Cohen et al., 2016; Geddes et al., 2018). While Geddes et al. found no reward-related enhancement of memory, Cohen et al. (2016) nevertheless found a robust effect of value on their behavioral memory measure. These results suggest that an alternate brain mechanism, instead of activation in the reward system, might account for value-related encoding selectivity when it is present in older adults.

An additional mechanism that seems to contribute to VDR in both younger adults and older adults is differential encoding. In both age groups, Cohen et al. (2014, 2016) observed increased activity in brain regions related to semantic processing, including left ventrolateral prefrontal cortex and left posterior lateral temporal cortex, during encoding of high-value information. Additionally, the magnitude of this increase in activity correlated with the degree to which value affected memory across both younger and older adults. This preservation of selectivity in the application of semantic strategies during encoding was interpreted to underlie older adults' preserved ability to preferentially encode high-value items in the VDR task. Other studies have further explored participants' ability to selectively attend to high-value items (Ariel, Price, & Hertzog, 2015; Robison & Unsworth, 2017) and use more effective learning strategies that involve associative and semantic processing (Ariel, Price, & Hertzog, 2015; Cohen, Rissman, Hovhannisyan, Castel, & Knowlton, 2017). These learning strategies produce a deeper and more elaborative encoding of semantic information that has been shown to improve memory performance (Craik & Tulving, 1975; Richardson, 1998). Common strategies include conjuring mental images of items, putting items in a sentence, or thinking about the relationship between items (Ariel, Price, & Hertzog, 2015).

In the present study, we used diffusion tensor imaging (DTI) to measure white matter characteristics along pathways that we hypothesized might be important in value-directed

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remembering for healthy older adults. Our primary tracts of interest were the inferior fronto-occipital fasciculus (IFOF) and the uncinate fasciculus (UF). The IFOF pathway extends ventrally from the orbitofrontal cortex to ventral occipital cortex (Catani & Thiebaut de Schotten, 2008). Notably, it connects the anterior temporal lobe, which has been extensively implicated as a domain-general processor of semantic information with modality-specific neural regions (de Zubicaray, Rose, & McMahon, 2011; see Patterson, Nestor, & Rogers, 2007 for a review). The IFOF has been shown in prior DTI studies to be involved in both the retrieval (de Zubicaray, Rose, & McMahon, 2011) and control of semantic information (Nugiel, Alm, & Olson, 2016), a conclusion further supported by lesion research (Harvey & Schnur, 2015) and examinations of functional connectivity (Turken & Dronkers, 2011). Additionally, many of the brain regions showing increased activity during encoding of high-value items in the present task, relative to encoding of low-value items, are connected via IFOF. These regions include portions of left lateral PFC, left posterior lateral temporal cortex, left parietal and bilateral occipital cortex (Cohen et al., 2016). Thus, it seemed probable that this white matter pathway would be involved in older adults' encoding of high-value words.

Our second tract of interest, the uncinate fasciculus (UF), was examined to determine whether the integrity of this pathway would be associated with memory for high-value items. In the young adult sample from the present value-directed remembering study, fractional anisotropy (FA) in uncinate fasciculus was shown to be positively correlated with the number of high-value items recalled (Reggente et al., 2018). This ventral pathway connects the anterior temporal lobe with the medial and lateral orbitofrontal cortex (Catani & Thiebaut de Schotten, 2008). White matter integrity in the UF is related to episodic memory (Lockhart et al., 2012), and like the IFOF, the UF has been associated with semantic processing (Matsuo et al., 2008; McDonald et

al., 2008; Acosta-Cabronero et al., 2011; de Zubicaray et al., 2011; Galantucci et al., 2011).

Thus, we expected that white matter connections instantiated in either IFOF or UF could be

important to semantic processing, and therefore to effective encoding of high-value words in

older adults.

We also examined the fornix because of its extensive role in memory and the changes it

undergoes in aging. The fornix is the primary efferent pathway from the hippocampus and it

connects the medial temporal lobe with the mammillary bodies and hypothalamus (Catani &

Thiebaut de Schotten, 2008). Higher fornical white matter integrity has been associated with

greater episodic memory and free recall performance (Grambaite et al., 2010; Metzler-Baddeley

et al., 2012) and recognition memory (Bennett & Stark, 2016). Furthermore, because white

matter integrity in the fornix often declines substantially in normal aging (Bennett & Stark, 2016;

Jang, Cho, Chang, 2011) and those with MCI (Metzler-Baddeley et al., 2012), older adults with a

relatively intact fornix may be at an advantage on the VDR task. It may also be the case that

activity in other regions during learning high value items may compensate for reduced white

matter integrity in the fornix in older adults.

Finally, integrity of the white matter tract connecting the NAcc to the VTA was

examined. These reward regions are part of a goal-directed loop that modulates learning (Lisman

& Grace, 2005), and they have been shown to be robustly connected (Krebs et al., 2011; Morales

& Margolis, 2017). In a recent DTI study using a probabilistic learning task, older adults who

performed comparably to younger adults had the greatest structural connectivity between NAcc

and VTA, and this connectivity was related to improved value representation in NAcc

(Chowdhury et al., 2013). Furthermore, Reggente et al. (2018) found that the robustness of this

pathway was correlated with greater memory selectivity and increased recall for high value

words in a sample of young adults performing the same VDR task as that used in the present study. However, given that older adults showed less value-induced modulation of activity in these reward-related regions during encoding (Cohen et al., 2016), we anticipated that the structural integrity of this pathway might not support memory for high-value items in older adults in the same way that it does in younger adults.

4.2 Method

4.2.1 Participants. Data from 25 older adults were collected for this study. Participants were recruited using flyers posted at the UCLA Medical Center and flyers and newsletter postings in West Los Angeles and the San Fernando Valley. Data from two participants were excluded from analysis due to neurological abnormalities observed in their MRI data (one cavernoma, one meningioma). The final sample of 23 older adults had an age range of 60 – 80 years ($M = 68.7$, $SD = 5.7$), and included 13 females and 10 males. These participants were all right-handed native English speakers with normal or corrected to normal vision. All participants scored at least 27 on an adaptation of the Mini-Mental State Exam (Folstein et al., 1975) indicating that they did not show major signs of dementia. Additionally, none of these participants had substantial neurological abnormality, as observed in their anatomical MRI scans, and none of them reported currently taking psychoactive medication for a psychiatric or neurological disorder. Informed consent was obtained and the study was run according to the guidelines of the UCLA Medical Institutional Review Board. Participants received \$15/h for participating.

Nineteen younger adults were used as a comparison group. They met similar inclusion requirements as the older adult sample. This sample included 10 females and 9 males (mean age = 21.8 years, $SD = 3.7$). Behavioral and fMRI data from both groups and DTI data from the

younger adult sample have been previously reported (Cohen et al., 2014; Cohen et al., 2016; Reggente et al., 2018), but the DTI analyses with older adults are reported here for the first time.

4.2.2 Design and Task Stimuli. On each study trial, participants were presented with an individual to-be-learned word that was preceded by a value cue denoting the number of points they would earn for later recalling that item. Their goal was to study the items such that they maximized their score. Each item was worth either a low (1, 2, 3) or high (10, 11, 12) value, with point-values chosen to produce the largest differences between low- and high-value items. Participants learned seven lists of words, with the first two lists considered as practice lists. Each list consisted of 24 unique words, with an equal number of items randomly assigned into each of the six possible point-values. The point-value associated with each word and list order were counter-balanced across participants. These word stimuli were 4-8 letter English nouns sampled from the Toglia and Battig (1978) word norms, clusters 6 and 7, and were rated as highly familiar (range: 5.5-7 on a 1-7 scale).

4.2.3 Procedures. Each participant completed the entire VDR memory task in the MRI scanner. Prior to scanning, participants were instructed about the memory task, and completed two practice lists with feedback. This extensive practice session was administered because selectivity is typically stronger on the third and subsequent lists (Ariel & Castel, 2014; Castel, 2008, McGillivray & Castel, 2011), as participants establish their learning strategy. During a study trial, participants viewed a value-cue for 2 s, saw a fixation cross jittered for 3-6.75 s, and then saw the word for 3.5 s. The value-cue was presented on a background designed to look like a gold coin. Afterwards, they saw a fixation cross for 1.5 s, and then completed a basic vowel-consonant judgment task for 3.75-8.75 s. In the vowel-consonant judgment task, 2 letters (50% of trials), 4 letters (25% of trials), or 6 letters (25% of trials) were presented sequentially in a

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pseudo-random order, with an approximately equal number of vowels and consonants presented. Each letter was shown for 1 s, followed by a 0.25 s fixation between letters. A 1.5 s blank screen was presented after the final letter. Each list began with 10 s of fixation, and ended with 15 s of the vowel-consonant task. Approximately 10-20 s after the end of each list, the participant was given 90 s to recall as many studied items as possible from the previous list. After each recall test, the participant was given feedback on the number of points earned on that list. This procedure was repeated across the two practice lists and five test lists.

4.2.4 Scanning Procedure. MRI data were acquired with a 3.0T Siemens Tim Trio Scanner at the UCLA Staglin IMHRO Center for Cognitive Neuroscience using a 12-channel receive-only phased array head coil. High resolution T1-weighted anatomical images were obtained using a 3D MPRAGE sequence with GRAPPA acceleration (TR = 1900 ms, TE = 3.26 ms, flip angle = 9°, FoV = 250 mm, 176 slices, voxel size = 0.98 x 0.98 x 1.0 mm). Diffusion weighted imaging data were obtained using a multi-directional weighted spin-echo echoplanar imaging (EPI) sequence (TR = 9000 ms, TE = 93 ms, 64 non-collinear directions, b-value = 1000 s/mm^2, echo spacing = 0.69 ms, FoV = 190 mm, 60 axial slices, voxel size = 2.0 x 2.0 x 2.0 mm) with a non-diffusion weighted reference volume (b-value = 0 s/mm^2). Prior to acquiring these structural scans, functional EPI data were obtained; findings from analysis of the functional data have been previously reported (Cohen et al., 2014; Cohen et al., 2016). Head movement was minimized by inserting extra cushions between the participant's head and the coil. Stimuli were presented using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA), and images were shown with either a custom-built MR-compatible rear projection system or MR-compatible goggles (Resonance Technology, Inc.).

4.2.5 Diffusion Tensor Imaging Data Processing. Older adult DTI data were processed using the same procedure described for the young adult dataset by Reggente et al. (2018). Briefly, diffusion weighted images (DWIs) were preprocessed using the FMRIB's Diffusion Toolbox (FMRIB Software Library, FSL version 5.0.9; http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL). First, all DWIs were corrected for eddy currents and aligned to the b0 reference volume. Second, the Brain Extraction Tool (BET) was used to generate brain-tissue-only masks for each subject that were applied to all images. Next, tensor models were fit to the diffusion data from each voxel to create subject-specific whole-brain maps of DTI metrics, specifically mean diffusivity (MD). We decided to test our hypotheses using MD, a measure that is sensitive to structural white matter damage and differences in axon density and diameter (Beaulieu, 2002), and is a particularly effective predictor of age-related memory impairment (Charlton, Barrick, Markus, & Morris, 2010). Additionally, compared with fractional anisotropy (FA), MD has been shown to be a more sensitive marker of age-related memory disorders including Alzheimer's disease and mild cognitive impairment (Acosta-Cabronero, Williams, Pengas, & Nestor, 2010; Bosch et al., 2012; Salat et al., 2010; Sexton et al., 2010). Moreover, FA is less likely to capture differences that occur when diffusivity is affected in multiple directions simultaneously, as is the case with age-associated demyelination (Bosch et al., 2012; Sexton et al., 2010).

Finally, FSL's BEDPOSTX was used to create an estimation of diffusion parameters at each voxel. This procedure uses a Markov-chain Monte Carlo sampling technique that accounts for crossing fibers to generate a Bayesian estimation of diffusion parameters at each voxel in a diffusion image (Behrens et al., 2003; Behrens et al., 2007). We leveraged this metric given that tract strength measures developed through DTI tractography have been shown to correlate

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strongly with anatomical connectivity determined using retrograde tracer injection (Donahue et al., 2016).

All analyses were computed in subject-specific diffusion space. Regions of interest (ROIs) used for calculating mean MD were initially mapped in Montreal Neurological Institute (MNI) space. These ROIs were first registered onto each subject's structural space (MPRAGE) using 12-parameter linear-affine registration using FMRIB's Linear Image Registration Tool (FLIRT). Next, FLIRT was used to bring these ROIs into subject-specific diffusion space using the non-diffusion-weighted b0 reference volume. Each subject-specific ROI registered in diffusion space was also examined visually and no major anatomical deviations were observed.

Our primary ROIs of interest—the left and right IFOF and UF—were defined based on the John Hopkins University (JHU) white matter tractography atlas (Hua et al., 2008; http://cmrm.med.jhmi.edu; Figure 1). Since IFOF and UF have substantial anatomical overlap, we decided to exclude all UF voxels from the IFOF masks and only analyze those portions that do not show overlap with UF (Reggente et al., 2018). Results for the full IFOF are also reported in Table 3. As structural integrity in the fornix has been associated with age-related memory performance (Grambaite et al., 2010; Metzler-Baddeley et al., 2012), a full fornix ROI was defined using the Jülich histological (cyto- and myelo-architectonic) atlas (Bürgel et al., 2006; http://www.fz-juelich.de/inm/inm-1/DE/Home/home_node.html) with a 50% probability threshold. An exploratory analysis of the basolateral amygdala was also computed as this area has been associated with reward learning in rodents and monkeys (Baxter & Murray, 2002). This ROI was also defined using the Jülich atlas with a 50% probability threshold. As a control analysis designed to rule out the possibility that generalized differences in white matter integrity correlated with our behavioral measures, we examined left and right corticospinal tract ROIs

defined from the JHU atlas. For all JHU atlas ROIs, we applied a 10% probability threshold to ensure sufficient coverage of each pathway, while avoiding excessive sparsity/shrinkage that would result if higher thresholds were applied.

To analyze structural connectivity between NAcc and VTA, we used the diffusion estimation generated by BEDPOSTX and FSL's PROBTRACKX to create a subject-specific metric of seed to target ROI connectedness. This procedure was carried out since no atlas for this pathway was publicly available. First, FreeSurfer's subcortical segmentation routine was used on each subject's MPRAGE scan to generate left and right NAcc ROIs. As the VTA is challenging to appropriately demarcate in T1-weighted MR images of individual subjects, a VTA ROI was defined for each subject using a probabilistic atlas of human VTA (Murty et al., 2014; http://web.duke.edu/adcocklab) with a 50% probability threshold. The pathway from each NAcc ROI to the VTA was calculated using 5000 samplings of the distribution of diffusion parameters from each voxel within a seed ROI; the distribution of streamlines was used to estimate a likely tract location.

Our measure of interest was the total number of samples from the seed ROI that reached the target mask. To control for variance in ROI size, we divided the total streamline count by the number of samples sent from the seed mask (i.e., 5000 * number of voxels in the seed ROI) (Johansen-Berg et al., 2005). Partial correlations, controlling for the size of the subject-specific target ROI, were computed between this tract strength value and memory measures of interest.
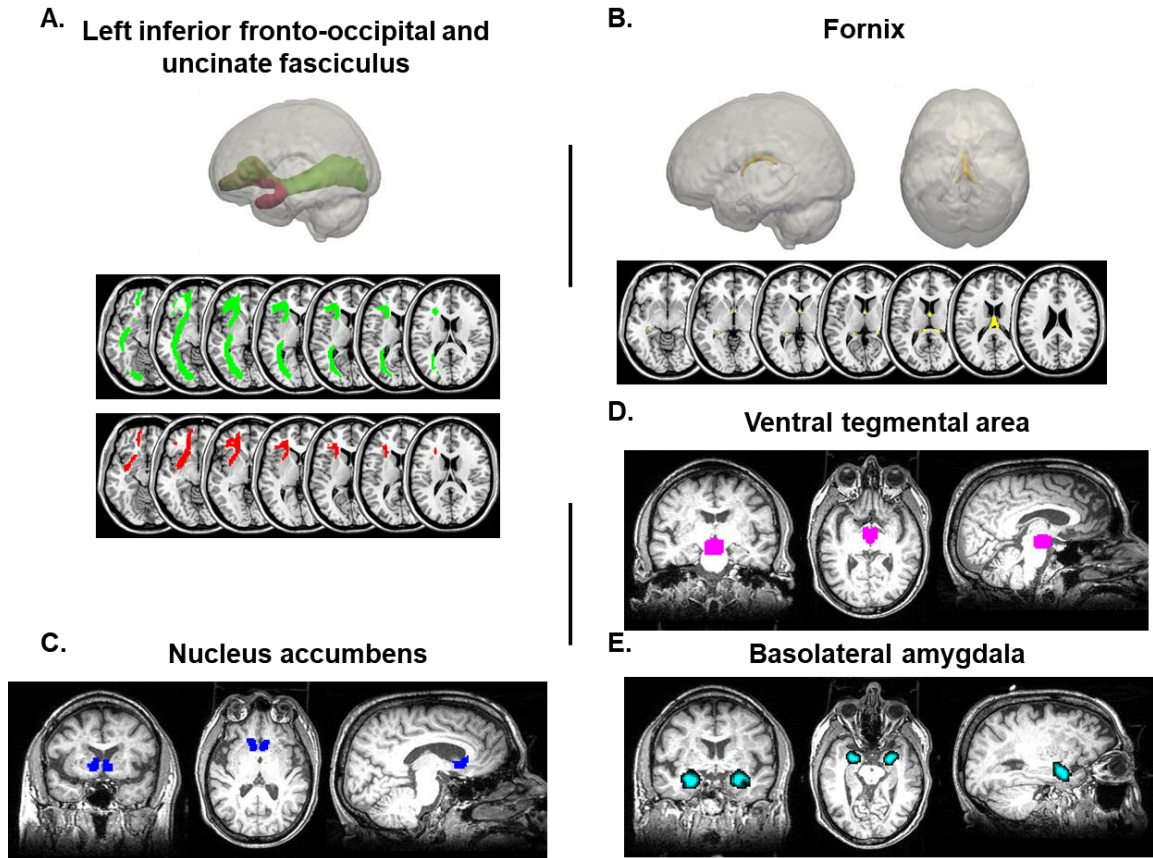
Figure 4.1. Regions of interest. **A)** Left inferior fronto-occipital fasciculus (green) and uncinate fasciculus (red) overlaid on a standard T1-weighted template in MNI space. Masks were defined using a probabilistic white matter tractography atlas (Mori et al., 2005). **B)** Fornix ROI defined using the same procedure. **C)** Nucleus accumbens (NAcc) ROI, aligned to and overlaid on a representative subject's MPRAGE. The NAcc was defined using FreeSurfer's automatic subcortical segmentation routine. **D)** Ventral tegmental area (VTA) ROI, aligned to and overlaid on a representative subject's MPRAGE. The VTA was defined using a probabilistic atlas of the human VTA (Murty et al., 2014). **E)** Basolateral amygdala defined using probabilistic white matter tractography atlas and aligned to and overlaid on a representative subject's MPRAGE.

4.2.6 Data Analysis. Statistical analyses were conducted using SPSS 22.0 (SPSS, Inc.,

Chicago, IL). Pearson correlation coefficients were computed between MD values for our tracts

of interest and our primary measures of memory performance: number of high-value items

recalled, number of low-value items recalled, and a measure known as the *selectivity index*

(Castel et al., 2002; SI). The SI reflects how selective a participant was in preferentially learning

and retrieving valuable items and is computed using the formula: (actual score – chance score) / (ideal score – chance score). A participant's achieved score is compared with the highest score they could have achieved given the number of items they retrieved (ideal score) and compared with chance performance (i.e., mean point-value multiplied by the number of words recalled). Each subject's SI was an average across all 5 lists presented in the MRI scanner, with the contribution of each list weighted by the number of items recalled. Within-group correlations between each behavioral measure and mean diffusivity in our six primary ROIs were controlled for multiple comparisons using a sequential Holm-Bonferroni method (Holm, 1979). To compare the strength of the relationship between a given region's MD and high-value and low-value item recall, a two-tailed test for the difference between two dependent correlations was used (Steiger, 1980).

4.3 Results

4.3.1 Behavioral Performance. Younger adults recalled significantly more items than older adults (Table 1). More specifically, younger adults recalled significantly more high-value items, though they did not significantly differ from older adults in recall of low-value items (for detailed behavioral results reporting, see Cohen et al., 2016). Nevertheless, strong value effects on memory were observed in both groups as the average selectivity index was significantly above 0 (i.e., with 0 representing value-insensitive recall) for both younger adults, $t(18) = 11.48$, $p < .001$, $d = 2.63$ and older adults, $t(18) = 6.12$, $p < .001$, $d = 1.28$.

Table 4.1. Recall Performance and Value-Selectivity Measures

	Younger Adults	Older Adults	t-statistic (df = 40)
Total Recall	11.83 (3.90)	7.63 (4.01)	3.42; $p = .001$
Low-Value Recall	3.18 (2.72)	1.99 (2.20)	1.57; $p = .125$
High-Value Recall	8.65 (1.87)	5.64 (2.79)	4.02; $p < .001$
Selectivity Index	.61 (.23)	.46 (.36)	1.52; $p = .136$

Note. Standard deviation in parentheses.

4.3.2 Memory Performance and White Matter Microstructure. Compared with the younger adult sample, older adults showed significantly higher MD values bilaterally in IFOF, UF, and the fornix suggesting that the integrity of these tracts was impaired with age (Table 2). To determine how these changes in MD may have influenced value-related selectivity, we first examined correlations between structural integrity (lower MD) and recall performance in these tracts. As the IFOF and UF overlap considerably, we examined MD in an IFOF mask with UF voxels removed. For older adults, lower MD in both left and right IFOF was significantly associated with increased recall of high-value items, but not low-value items (Table 3, Figure 2). The difference in correlation magnitude between high-value and low-value items was a marginal trend for left IFOF, $z = 1.92$, $p = .055$, but was not significant for right IFOF, $z = 1.57$, $p = .116$. For younger adults, MD of the IFOF was not significantly correlated with recall of either item type (all p's > .396). Results for the full IFOF, without the UF exclusion, show a similar pattern (Table 3).

Table 4.2. Tract-specific measures of mean diffusivity

	Younger Adults	Older Adults	t-statistic (df = 40)
IFOF, left	0.83 (0.03)	1.02 (0.14)	5.64; $p < .001$
IFOF, right	0.84 (0.03)	1.00 (0.10)	6.75; $p < .001$
UF, left	0.86 (0.06)	1.00 (0.10)	5.25; $p < .001$
UF, right	0.93 (0.06)	1.10 (0.11)	6.12; $p < .001$
Fornix	1.59 (0.26)	2.29 (0.46)	5.81; $p < .001$

Note. Mean diffusivity (x 10^{-3} mm^2/s). Standard deviation in parentheses.
IFOF = inferior fronto-occipital fasciculus; UF = uncinate fasciculus
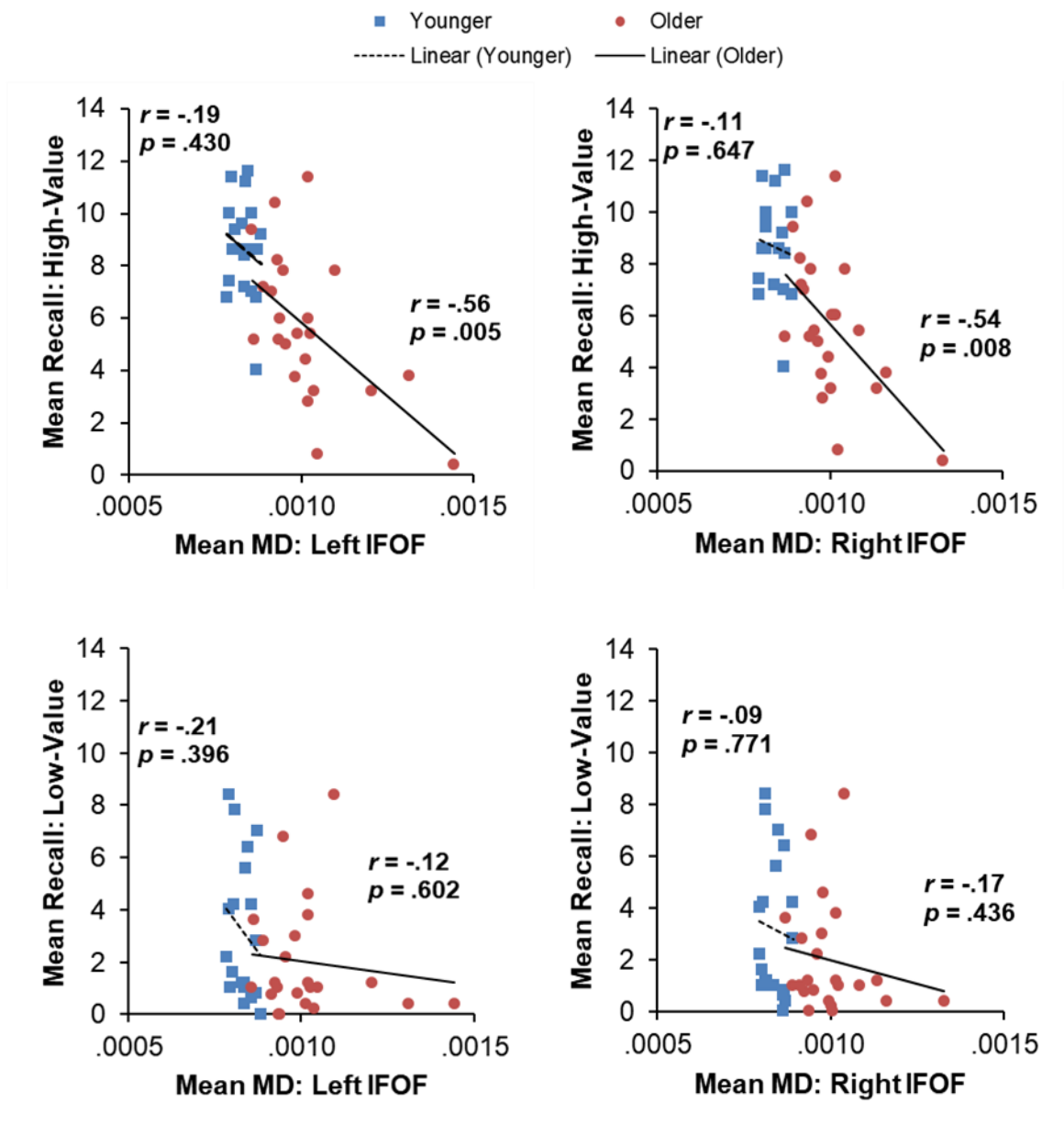
Figure 4.2. Recall of high-value and low-value items by mean diffusivity in left and right IFOF. Correlation statistics presented for younger adults (left) and older adults (right). MD = mean diffusivity; IFOF = inferior fronto-occipital fasciculus

The observed relationships between memory for high-value items and MD of the left and right IFOF in older adults survived controlling for multiple comparisons. Because we observed an outlier with MD over 2 standard deviations above the mean for the IFOF ROIs, and almost 2 SD below the mean on high-value recall, we also examined these associations using Spearman's

rank correlation coefficient. Unlike the Pearson correlation, this non-parametric measure is highly robust to the effects of outliers (Croux & Dehon, 2010). Significant relationships between high-value recall and MD were still observed in both left IFOF (ρ = -.56, p = .006) and right IFOF (ρ = -.48, p = .022). Thus, the findings in IFOF do not appear to be due to the influence of outliers.

To determine whether high microstructural integrity of the IFOF in older adults supports strategic learning of high-value items, the correlation magnitude between IFOF MD and high-value recall was examined by study list. As value-related selectivity in recall increases across study lists—see Cohen et al., 2016 for a detailed description of these findings—participants likely develop effective strategies for selective learning after completing the first few study lists (e.g., Cohen et al., 2017). The correlation magnitude between IFOF MD and high-value item recall does generally increase across lists (Figure 4.3). However, in left IFOF, when the magnitude of the correlation for the first two lists (M = .46) and last two lists (M = .52) are compared, the increase in correlation magnitude is not statistically significant, z = 0.47, p = .641. Likewise, in right IFOF the difference in correlation magnitude for the first two lists (M = .47) and last two lists (M = .49) is not significant, z = 0.14, p = .892.
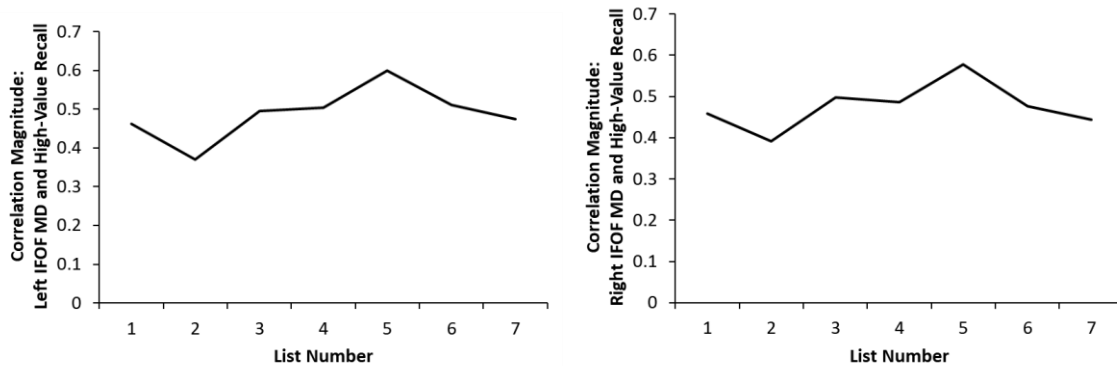
Figure 4.3. Absolute value of the correlation between high-value item recall and MD in the left IFOF (left) and right IFOF (right) across study lists 1-7 in older adults. IFOF = inferior fronto-occipital fasciculus

Next, correlations between MD in the UF and fornix with recall were examined in each age group. As Reggente et al. (2018) reported using FA as a measure, stronger microstructural integrity in both left and right UF (as evidenced here by lower MD) was associated with increased recall of valuable items in younger adults. However, we observe no such correlation in either hemisphere in older adults (Table 3). For younger adults, the difference in correlation magnitude between high and low-value items was significant for left UF, $z = 2.52$, $p = .012$, and had a strong trend for right UF, $z = 1.92$, $p = .055$. For older and younger adults, MD in the fornix was not significantly associated with either high-value or low-value item recall, all r's < .13, all p's > .3 (Table 3). As a control analysis, MD of the corticospinal tract was examined. MD was not significantly correlated with high-value recall, low-value recall, or selectivity index in either age group, all r's < .24, all p's > .1. Note that selectivity index was not significantly associated with MD in any of the above tracts, all r's < .33, all p's > .1.

Table 3. Pearson correlations between recall measures and mean diffusivity in tracts of interest, and comparison tract (CST), for younger and older adults

	IFOF* left	IFOF* right	IFOF left	IFOF right	UF left	UF right	Fornix	CST left	CST right
Younger adults									
High-value	-.19	-.11	-.33	-.24	**-.64**[b]	-.52[c]	.03	-.12	-.24
Low-value	-.21	-.09	-.31	.34	-.07	-.05	-.05	-.08	-.14
SI	.26	.25	.19	.18	-.28	-.25	.18	.15	.12
Older adults									
High-value	**-.56**[b]	**-.54**[b]	-.49[c]	-.60[b]	-.12	-.16	-.12	-.04	.01
Low-value	-.12	-.17	-.12	-.18	.20	.02	-.01	.06	-.03
SI	-.20	-.14	-.17	-.19	-.33	-.23	-.14	.03	.15

Note. SI = selectivity index; IFOF = inferior fronto-occipital fasciculus; IFOF* = IFOF (UF voxels excluded); UF = uncinate fasciculus; CST = corticospinal tract
[a]correlations that reached significance level controlled for multiple comparisons using the Holm-Bonferroni procedure are highlighted in bold.
[b]$p < .01$
[c]$p < .05$

4.3.3 Memory Performance and Reward Circuit Tract Strength. Next, contributions of the NAcc-VTA reward circuit to VDR were examined. Similar to Reggente et al. (2018), we combined the left and right NAcc ROIs into a single bilateral NAcc mask and assessed the relationship between the mean NAcc-VTA tract strength with our recall measures. Partial correlations are reported controlling for the size of the VTA target ROI. Mean tract strength did not significantly differ between older adults ($M = .015$, $SD = .018$) and younger adults ($M = .014$, $SD = .014$), $t(40) = 0.26$, $p = .797$, $d = 0.08$. For younger adults, NAcc-VTA tract strength was significantly associated with recall of valuable items, but not low-value items, and this difference in correlation magnitude was significant, $z = 2.78$, $p = .005$. Tract strength did not significantly correlate with memory for either item type in older adults (all p's > .659). To determine if this null effect in older adults was due to small sample size, we conducted a post-hoc power analysis using GPower (version 3.0; Heinrich Heine Universität Düsseldorf;

http://www.gpower.hhu.de/en.html) with the effect size observed in younger adults ($r = .51$). This study had an estimated power of .77 to observe a comparable significant relationship between NAcc-VTA tract strength and valuable item recall in older adults.

 4.3.4 Exploratory Examination of Basolateral Amygdala. Lastly, microstructural integrity of the basolateral amygdala and memory performance were examined for older adults. Mean diffusivity of the left ($r = -.12$, $p = .573$) and right ($r = -.19$, $p = .376$) basolateral amygdala were not associated with memory for high-value items. However, higher FA in the left ($r = .45$, $p = .031$) and right ($r = .44$, $p = .036$) basolateral amygdala were associated with greater memory for high-value items. In contrast, neither MD nor FA in the basolateral amygdala were associated with memory for low-value items (all r's < .17, all p's > .427).

4.4 Discussion

 In the current study, diffusion tensor imaging was used to determine whether individual differences in the microstructural integrity of white matter tracts in older adults is related to their ability to selectively encode and retrieve valuable information. Most notably, higher white matter integrity (lower MD) in bilateral IFOF was associated with increased memory for valuable items in older adults. In contrast to the findings from the younger adult sample who completed the same task, we did not find a relationship between memory performance and white matter integrity in UF, nor did the older adult sample show a significant relationship between NAcc-VTA tract strength and memory for valuable items. These findings are discussed in detail below.

 The IFOF is part of a semantic processing network (Binder & Desai, 2011) that connects frontal regions involved in goal-directed learning and retrieval search (Dobbins & Wagner, 2005; Skinner & Fernandez, 2007) with temporal and occipital cortices involved in semantic and visual processing (Catani & Thiebaut de Schotten, 2008). In line with our predictions, MD in both left

and right hemisphere IFOF was significantly related with older adults' memory for high-value items but not low-value items. Older adults also showed significantly higher MD in the IFOF relative to younger adults, suggesting the presence of moderate age-related white matter atrophy. For the younger adult sample, MD in the IFOF was not correlated with these measures of recall. In the value-directed remembering task, more items are presented than participants can remember; to optimize their performance, they must selectively encode only the most valuable items. The agenda-based regulation framework posits that time, resources, and effort are allocated based on a goal-oriented agenda that aims to maximize performance (Ariel, Dunlosky, & Bailey, 2009; Dunlosky & Ariel, 2011; Middlebrooks, Kerr, & Castel, 2017). In accordance with this framework, both older and younger adults report selectively using elaborative semantic encoding strategies when learning valuable items (Ariel, Price, & Hertzog, 2015; Cohen et al., 2017). The current findings suggest that, particularly in older adults, integrity of the IFOF may account for significant variance in this enhanced semantic processing of valuable items. Functional MRI data from this same set of subjects showed that older adults had increased activity in left VLPFC, left lateral temporal cortex, and bilateral occipital cortex during encoding of valuable words (Cohen et al., 2016). Based on its anatomical location (Catani & Thiebaut de Schotten, 2008), the IFOF is a prime candidate for coordinating these regions during value-directed remembering.

A second key finding was that tract strength in the NAcc-VTA reward circuit, measured via probabilistic tractography, was not correlated with memory for valuable items in older adults. Additionally, older adults did not significantly differ from younger adults on NAcc-VTA tract strength. This neural pathway is activated in response to anticipated rewards (Adcock et al., 2006) and modulates the encoding of information into long-term memory via its dopaminergic

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inputs to the hippocampus (Bethus, Tse, & Morris, 2010; Lisman & Grace, 2005; Rossato et al., 2009). Younger adults in this experiment did show a significant relationship between higher NAcc-VTA tract strength and improved memory for valuable items (Reggente et al., 2018). One plausible reason why this relationship was not significant in older adults is that normal aging is associated with a substantial decline in the amount of striatal dopamine transporters and receptors (Kaasinen & Rinne, 2002; Karrer, Josef, Mata, Morris, & Samanez-Larkin, 2017). More specifically, aging is associated with reduced amounts of D_1 and D_2 receptors (Düzel, Bunzeck, Guitart-Masip, & Düzel, 2010; Rinne, Lönnberg, & Marjamäki, 1990; Wang et al., 1998), with loss of both receptors types estimated to be between 2-5% a decade (Rinne et al., 1990; Seeman et al., 1987). During probabilistic reward learning, neural correlates of reward prediction error are reduced in older adults (Samanez-Larkin, Worthy, Mata, McClure, & Knutson, 2014), and these impairments are mitigated by administration of L-dopa, a dopamine agonist (Chowdhury et al., 2013). Thus, declines in the availability of dopamine may limit the extent to which activation in reward circuitry supports value-driven encoding and recall in older adults. Although we did not observe age-related differences in the structural integrity of the NAcc-VTA tract, functional differences in this tract may have caused older adults to rely on different neural ensembles to successfully perform the task.

Finally, the integrity of white matter in UF did not correlate with memory performance in older adults, in contrast to what Reggente et al. (2018) observed in younger adults. In prior research, UF integrity has been associated with reward sensitivity (e.g., Camara et al., 2010; Bjornebekk et al., 2012), verbal episodic memory (Niogi et al., 2008), processing of semantic information (de Zubicaray et al., 2011), and with interactions between these systems (Von der Heide, Skipper, Klobusicky, & Olson, 2013). Reggente et al. concluded that the correlation

between UF integrity and recall of high-value information in the VDR task was likely due to UF having a role in control of semantic information processing. This tentative conclusion was based on the observation that NAcc-VTA tract strength correlated with selectivity index, a measure of reward sensitivity in this task, while UF FA values showed no such correlation. It is possible that, although individuals in both age groups appear to modulate semantic processing as a function of item value, there are still subtle but important differences in how they do so. Cohen et al. (2016) found that in both younger and older adults, value-related differences in brain activity in a semantic network correlated with memory selectivity. However, they also found that younger adults who increase activity in the semantic network for high-value items show improved value-related selectivity, whereas older adults who decrease activity for low-value items show improved value-related selectivity. This distinction may hold explanatory value for the present findings.

A possible explanation for the divergent findings across age groups is that, in younger adults, the correlation between UF integrity and high-value recall reflects the ability to integrate cue information signaling a high reward value with the semantic knowledge that enhances encoding of high-value words (Von der Heide et al., 2013). In other words, young adults with stronger UF connectivity may be more motivated and/or better able to implement semantic encoding strategies for high-value items. In contrast, in older adults, semantic processing seems to occur independently of activity in the dopaminergic reward system; the reward system is not selectively activated on high-value items, and memory selectivity seems to be mediated by a strategy-driven reduction in semantic encoding when learning low-value items, not by enhanced motivation to learn high-value items (Cohen et al., 2016). Thus, it is plausible that in older adults, individual differences in the ability to successfully engage semantic encoding processes

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on high-value words would rely on white matter fiber connections that are less strongly associated with processing emotional/reward valence. Consistent with this suggestion, recent work has proposed that the IFOF is the primary tract responsible for processing of semantic information, with the UF typically playing a more supplementary role (Duffau, Herbet, & Moritz-Gasser, 2013; Nugiel, Alm, & Olson, 2016). We can speculate that if not for the involvement of the reward system in motivating semantic encoding of high-value words in younger adults, both age groups might show a correlation between IFOF integrity and performance in our verbal free recall task.

Mean diffusivity of the basolateral amygdala was also not correlated with memory for high-value items in older adults, though higher FA in this region was associated with better memory for high-value items, but not low-value items. Although this analysis was exploratory and would not survive controlling for multiple comparisons, the basolateral amygdala plays an important role in storing and updating stimulus—value associations in monkeys (see Baxter & Murray, 2002 for a review) and it seems likely that it is also involved in the selective encoding that takes place in VDR tasks. Sometimes important information is highly emotionally arousing; for example, we might like to remember a delightful honeymoon in the Caribbean or what street we were on when our wallet was stolen. Functional MRI research suggests that memory is strengthened for emotional images due to recruitment of the amygdala and strong connections between the amygdala and the hippocampus (Dew, Ritchey, LaBar, & Cabeza, 2014). The current findings suggest that the amygdala likely also plays a role in remembering information that is important yet much less emotionally arousing.

Because older adults showed largely intact value-directed remembering, but no significant relationship between the structural integrity of the NAcc-VTA pathway and this

selective learning, it may also be the case that semantic processing strategies relying on IFOF help to compensate for the lack of reward responsivity. Younger and older adults selectively use elaborative strategies when learning valuable items (Ariel, Price, & Hertzog, 2015) that promote semantic processing (Craik & Tulving, 1975; Richardson, 1998) and result in increased episodic binding (Hennessee, Knowlton, & Castel, 2018). Additionally, when presented with a large amount of information, older adults often report ignoring low-value items (Ariel, Price, & Hertzog, 2015) or allocate substantially more study time to valuable items (Castel, Murayama, Friedman, McGillivray, & Link, 2013). This goal-directed allocation of attention may be particularly important for older adults.

One limitation of the current study was the relatively small older adult sample size (although this sample size is comparable to other fMRI and DTI studies with older adult samples, see Geddes et al., 2018). Fortunately, our main finding in IFOF was both large in magnitude and survived controlling for multiple comparisons. However, because our findings regarding the NAcc-VTA reward pathway were based on a null effect, this analysis in particular should be replicated in future research to rule out the possibility of a false negative. That said, the lack of a relationship between the NAcc-VTA pathway integrity and VDR performance parallels the lack of BOLD signal activation in this system in older adults in the VDR task (Cohen et al., 2016). The small sample size also means that the lack of correlation with VDR performance and MD in the UF and fornix should also be interpreted cautiously. With larger samples and greater power, it may be possible to detect a potential relationship between memory for high-value items and integrity of tracts involving the hippocampal system.

4.4.1 Conclusions. This study provides novel evidence that greater microstructural white matter integrity in the IFOF is associated with increased value-selective encoding and retrieval in

healthy older adults. Unlike younger adults, older adults did not show a significant relationship between either UF white matter integrity or tract strength in the NAcc-VTA reward circuit and memory for valuable items. The IFOF may be supporting a compensatory role of enhanced deep encoding during motivated learning in aging.

Chapter 5

General Discussion

Across these three studies, a wealth of information has been discovered regarding how aging affects VDR and how younger and older adults may rely on different cognitive and neurological mechanisms in selectively learning valuable information. The first study (Chapter 2) examined how selectively learning valuable material influences the quality of memory in younger and older adults, focusing on measures such as hit rate, confidence, recollection, and memory for associated details. The second study (Chapter 3) examined the relative contributions of strategic and automatic processing to value-directed recognition. Finally the third study (Chapter 4) was designed to determine whether individual differences in the microstructural integrity of white matter tracts can explain why some older adults are excellent at selectively learning valuable information, whereas others are not. Over the next few pages, I will discuss how the novel findings of these three studies might be integrated and how they contribute to our understanding of age-related changes to VDR.

5.1 Effects of Value-Directed Remembering on the Quality of Memory

In all three studies, we have observed strong evidence that participants selectively encode and later recognize valuable material. Importantly, older adults in Study 1 and Study 3 demonstrated strong VDR, which supports the general consensus that this selective learning is intact in normal aging (Castel et al., 2013; Cohen et al., 2016; Spaniol, Schain, & Bowen, 2013). Considering that older adults displayed worse recognition memory across these experiments, their selective encoding of valuable information is highly adaptive. The current findings are novel in that they show that these VDR effects in older adults extend to recognition memory. Much of prior VDR research has tested memory using free recall. Selective encoding seems less

critical in the context of recognition testing, because although only a relatively small number of items can be retrieved via free recall, the number of items that can be recognized is much less limited. Prior research has shown that free recall is limited by one's working memory capacity (Linderholm & van den Broek, 2002; Unsworth, 2007), whereas recognition memory for individual pictures after a single exposure is nearly limitless (Standing, 1973). Additionally, because the study lists that were used were considerably longer than typical recall study lists, if participants were selectively using elaborative learning strategies, these effortful strategies would need to be maintained across a longer period. Indeed, some studies using short retention intervals have not observed value effects on recognition memory (e.g., Spaniol, Schain, & Bowen, 2013). These VDR effects are also often smaller when participants expect a recognition test as opposed to a recall test (Middlebrooks, Murayama, & Castel, 2017), which supports that metacognitive control processes play an important role in VDR. In light of these characteristics of recognition memory testing, although the VDR effects described in the current studies were somewhat smaller than what is observed with free recall, it is noteworthy that these effects of value on memory were still robust. When VDR is examined via free recall, it is challenging to determine the extent that value enhances encoding versus the extent that valuable items are simply reported first. For example, if during the recall test a participant could bring multiple items to mind, they would likely desire to report the more valuable items first to avoid them fading from working memory. Because recognition testing essentially randomizes the order that items are (or are not) retrieved from memory, the current findings provide additional support that value affects later retrieval by enhancing encoding.

Although valuable items were more likely to be recognized at test, they were also associated with higher confidence ratings, though this effect of value on confidence was

somewhat less consistent. In the first experiment of Study 1, older adults gave lower confidence ratings than younger adults. However, older adults, but not younger adults, displayed significantly higher confidence ratings for valuable items. This value effect on confidence brought older adults' confidence ratings for valuable items closer to the confidence levels reported by younger adults. In the second experiment, items with high objective-value (i.e., items congruent with an imagined state of physiological need) were recognized with higher confidence in both age groups, whereas items high in subjective-value (i.e., how much did they want the object) did not show this effect on confidence. Effects of item-value on confidence appear to be more complex in younger adults, as prior research has shown both null and small effects of value on recognition confidence (Hennessee, Castel, & Knowlton, 2017), though both in that study and in the second study of this dissertation, younger adults were more likely to give the highest confidence response ("Definitely Old") for valuable items. Taken together, these findings suggest that when valuable items are selectively encoded it produces a stronger memory trace that can more confidently be retrieved. Previous research suggests older adults are less confident in their recognition responses (e.g., Spaniol, Schain, and Bowen, 2013), as was observed in this dissertation, though they appeared to more consistently demonstrate this value-based enhancement of recognition confidence. When older adults selectively learn valuable information, this selective encoding may mitigate some of their age-related decline in recognition confidence.

Effects of VDR on memory were also examined using a Remember-Know-Guess (R-K-G) paradigm. Aging, both for healthy adults and for those with memory disorders such as mild cognitive impairment and Alzheimer's disease, is associated with strong declines in episodic memory that are observable using this R-K-G design and measures of source memory (see Koen

& Yonelinas, 2014, for a review). Specifically, experiences of recollection and memory for source details decline considerably in aging though familiarity shows only a modest decrease that is inconsistent across studies. Previous research suggests that when valuable items are selectively learned, they are more likely to be associated with experiences of recollection at test, though effects of value on familiarity are small and inconsistent (Hennessee, Castel, & Knowlton, 2017). This pattern of results was replicated in the current studies, as younger adults in the first and second studies demonstrated increased recollection when recognizing valuable items. Somewhat surprisingly, despite that older adults typically show deficits in recollection, we observed that this effect of value on recollection was preserved in aging. The magnitude of this effect was found to be comparable for both age groups, as the Age x Item-value interaction was not found to be statistically significant. Value appears to enhance memory by strengthening recollection and this mechanism is preserved in healthy aging.

Finally, value's effect on memory was assessed by examining memory for associated details (i.e., point-value, word color, or imagined location; Chapter 2). Given that younger and older adults displayed similar effects of value on recognition and recollection, and older adults appeared to display a stronger effect of value on confidence, one might expect value to influence memory for associated details in a similar manner across these two age groups. However, although both age groups showed significantly better memory for point-values associated with valuable items than with low-value items, only younger adults demonstrated better memory for the location of items high in objective-value. One plausible explanation is that binding words with their respective point-values may have been relatively easy for older adults as this information was presented simultaneously. In contrast, in Study 2 Experiment 2, there was a 4 s delay between the presentation of the imagined location and the target item. Binding the item

with the location would require them to effectively maintain the location in mind during this period; because working memory capacity declines in normal aging (see Salthouse, 1994 for a review), we would expect maintaining this information to be more difficult for older adults. This interpretation is also supported by the fact that older adults were less likely to retrieve the item location overall, and previous research suggests that older adults often show declines in remembering source details (Koen & Yonelinas, 2014). This deficit in item-location binding, which was particularly strong for valuable items, may be problematic as valuable objects are often only useful if one can retrieve their location. For example, if a person is hungry and they know that they have an energy bar, that snack is only useful for them if they can correctly remember where they last had it.

The present findings have important implications for theories of VDR. First, older adults' strong VDR extends to recognition testing with a short retention interval. This supports that their enhanced retrieval of valuable information is due to differences in encoding between valuable and low-value items. Second, both younger and older adults show stronger and more vivid memories of valuable items, as observed by increased recollection and recognition confidence. Third, this selective encoding enhances the binding of task-relevant details to items often at the expense of poorly encoding extraneous details. However, this binding of task-relevant details to valuable items appears to be less robust in older adults, as evidenced by their poor memory for imagined locations associated with valuable items.

5.2 Contributions of Strategic and Automatic Mechanisms to Value-Directed Remembering

Having first examined the effects of value on recognition memory, recollection, and associative binding, and whether these effects change in aging, my next goal was to determine

which mechanisms may be supporting VDR. The literature is relatively divided on this topic.

Many researchers argue that VDR occurs primarily because learners selectively encode items via a differential use of elaborative encoding strategies (Ariel, Price, & Hertzog, 2015; Cohen et al., 2017) or a goal-directed allocation of attention and study time (Ariel, Dunlosky, & Bailey, 2009; Dunlosky & Ariel, 2011; Castel et al., 2013). Other researchers have instead focused on how item-value elicits differences in neural processing that may enhance encoding in a relatively automatic fashion. For example, high value cues activate a dopaminergic system that selectively enhances the long-term maintenance of memory in the hippocampus (Adcock et al., 2006; Carter et al., 2009; Lisman & Grace, 2005). Study 2 (Chapter 3) was designed to determine the relative contribution of these strategic and more automatic processes. In the first experiment, participants completed a directed-forgetting task wherein items differed in point-value. The contributions of elaborative encoding, maintenance rehearsal, and a potentially automatic process were examined by manipulating whether the cue occurred after a short or long delay. In younger adults, high-value items paired with immediate forget cues were recognized substantially more often than low-value items paired with immediate forget cues. Because a strong directed-forgetting effect was observed in this study and items paired with an immediate forget cue receive substantial inhibition at encoding (Bjork, 1989; Wylie, Fox, & Taylor, 2007), the most likely interpretation is that a relatively automatic process is contributing to memory for valuable items. Although recognition memory was much stronger for to-be-remembered items than to-be-forgotten items, we did not observe a significant improvement in memory on trials that supported the maximal use of elaborative encoding strategies (immediate remember cue). In a second experiment, the directed-forgetting paradigm was removed, and three between-subjects groups were either given no instructed regarding how to learn items, or were instructed to use a mental imagery or mental

rehearsal strategy to encode all items. We observed a strong effect of value on recognition even when participants were instructed to learn all items via mental rehearsal. It is likely that a relatively automatic process contributed to the encoding of these items. As participants in this condition still reported using elaborative strategies, including mental imagery and putting words in sentences, it is also possible that they used these more effective strategies to learn valuable items.

From the above findings, it appears an automatic process is contributing to value's effect on recognition memory. One very likely candidate is a value-based modulation of the hippocampal-VTA loop (see Lisman & Grace, 2005 for a review). In this loop, the hippocampus signals the presence of novel stimuli. Next, the NAcc and VTA—in concert with goal-directed activation in frontal cortices—signal whether the stimuli is important and potentially predictive of reward (Adcock et al., 2006; Chowdhury et al., 2013). Finally, VTA neurons provide a dopaminergic signal to the hippocampus that has been shown to be necessary for maintenance of information in long-term memory (Bethus, Tse, & Morris, 2010; Rossato et al., 2009). This is a system of great evolutionary importance, as humans and other animals need to be able to remember valuable stimuli and cues that predict later reward. We have reason to believe that this hippocampus-VTA loop is accounting for the automatic effects of value that we observed in younger adults, as looking at high value cues has been shown to increase activity in bilateral NAcc, VTA, and large swaths of frontal and parietal cortices (Cohen et al., 2014). Furthermore, recent DTI research suggests that higher microstructural integrity of the NAcc-VTA tract in younger adults is associated with higher value-related selectivity on a free recall VDR task (Reggente et al., 2018).

In the older adult sample reported in Study 2, we did not observe significant value effects on memory for items paired with immediate forget cues, suggesting that older adults do not rely on automatic processing in the hippocampus-VTA loop to the same extent as younger adults. This pathway may play a diminished role in older adult VDR as normal aging is associated with a substantial decline in the amount of striatal dopamine transporters and receptors (Kaasinen & Rinne, 2002; Karrer, Josef, Mata, Morris, & Samanez-Larkin, 2017). In line with this interpretation, older adults completing probabilistic reward learning tasks have been shown to have an impaired representation of reward prediction errors in the striatum (Samanez-Larkin et al., 2014) and that administration of L-dopa, a dopamine agonist, is associated with an improvement in learning and these neural correlates of reward prediction (Chowdhury et al., 2013). Additionally, in Cohen et al. (2016) older adults did not show significant activation of NAcc or VTA in response to high-value cues. Finally, in Study 3 of this dissertation, the microstructural integrity of the NAcc-VTA tract was not significantly associated with value-related selectivity in older adults. As this sample also did not show significant structural atrophy in this tract, it may be that functional changes to this tract, perhaps brought about by reduced dopamine levels, caused them to rely on other neural ensembles to selectively encode valuable information. Overall, the above research provides considerable support for a diminished role of the hippocampus-VTA loop in older adult VDR. The hippocampus-VTA loop is likely enhancing encoding of valuable items for younger adults in a relatively automatic fashion, whereas older adults likely must rely more on deliberate selective encoding strategies.

Next, the role of elaborative encoding processes in VDR was examined. In the first experiment of Study 2, when participants were asked to encode all items using mental imagery, value's effect on recognition, confidence, and recollection was substantially diminished. More

specifically, this is because use of mental imagery significantly improved these three measures

for low-value items to the extent that memory for both item-types was comparable. Because

mental imagery promotes a more elaborative semantic encoding of items, this suggests that

value's effect on memory is at least partially explained by value-based differences in semantic

processing. The findings of Study 3 further support this role of semantic processing in VDR.

These DTI results suggest that older adults with greater structural integrity in bilateral IFOF and

younger adults with greater structural integrity in the uncinate fasciculus (UF) have higher value-

related selectivity on the VDR task. Previous research implicates both the IFOF and UF in

semantic processing (Binder et al., 2009; Binder and Desai, 2011; de Zubicaray et al., 2011;

Galantucci et al., 2011), likely because they extend through the anterior temporal lobe, which is a

domain-general processor of semantic information (de Zubicaray, Rose, McMahon, 2011;

Patterson, Nestor, & Rogers, 2007). In a study examining the correlates of effective VDR, older

adults, but not younger adults, displayed a strong correlation between working memory capacity

and their ability to selectively learn valuable information (Castel, Balota, & McCabe, 2009). This

suggests that VDR in older adults is limited by their capability to use strategic control during

encoding. Furthermore, older adults with behavioral-variant frontotemporal dementia, a disorder

known to strongly impair strategy use (Pasquier, Grymonprez, Lebert, & Van der Linden, 2001),

have shown a lack of selectivity in VDR (Wong et al., 2018). Overall, this research strongly

demonstrates that VDR is supported by semantic processing that selectively benefits the

encoding of valuable items. Furthermore, it appears that the role of strategic control during

encoding is particularly important in older adults.

It should be noted that one of the current experiments did not provide support for a strong

role of elaborative encoding in VDR. In the first experiment of Study 2, both younger and older

adults did not display better memory for items paired with an immediate remember cue versus those paired with a cue that was delayed by 5 s. Items paired with an immediate remember cue provided the maximum potential for participants to utilize deliberate elaborative encoding strategies, thus this finding suggests that using lengthy elaborative encoding strategies is not necessary for VDR. Because mental rehearsal was the most prevalently reported encoding strategy in the Experiment 2 No Instruction condition, it may be that participants did not benefit from the increased time because they were using a relatively inefficient learning strategy (Ariel, Price, & Hertzog, 2015). Alternatively, considering the strong directed-forgetting effect in Experiment 1, it may be that participants paid more attention to the directed-forgetting cue than item-value. Because prior VDR research suggests that younger and older adults differentially apply elaborative semantic encoding strategies based on item-value (Ariel, Price, & Hertzog, 2015; Cohen et al., 2017), as does the rest of this dissertational research, it seems likely that elaborative encoding plays an important role in VDR.

5.3 Future Directions

Additional research is necessary to further our understanding of VDR and how it changes in aging. First, additional research should be conducted to determine whether these effects of value on confidence, recollection, and memory for associated details generalize to other memory testing formats, such a word-pair and free recall testing. Since VDR effects are usually larger on free recall tests (Cohen et al., 2017), it is uncertain whether effects of value on recollection would also be larger. Second, additional research should examine strategic and neural mechanisms that support VDR. Although research on these topics has been growing lately, many important findings have not been sufficiently replicated or supported. This is most acutely demonstrated by the scarcity of DTI research on VDR and the limited number of studies that

have investigated elaborative strategy use in VDR. Third, as our ability to remember valuable information is critical to effective learning in everyday life, deficits in VDR for those with Alzheimer's disease, frontotemporal dementia, and mild cognitive impairment should be investigated in more detail. Recent research by Wong et al. (2018) suggests that deficits in VDR for patients diagnosed with Alzheimer's disease or behavioral-variant frontotemporal dementia can be quite severe. Any treatments or lifestyle changes that counteract these VDR deficits may go a long way to improving older adults' quality of life.

5.4 Conclusions

Overall, this dissertational research demonstrates that VDR has robust and powerful effects on recognition memory and that the neurological mechanisms that support these effects change in aging. Item-value at encoding is associated with improved recognition memory, higher confidence, and greater recollection and these effects were observed across a wide range of manipulations and for both words and pictures. These effects were observed to be preserved in healthy aging. Selectively encoding valuable items was also associated with increased binding between items and task-relevant details, though older adults did not show this effect for item-location binding. These value-based enhancements of memory appear to be due to relatively automatic processing in the hippocampus-VTA for younger adults, though older adults may need to instead rely on semantic processing in the IFOF. Age-related changes in the availability of dopamine may cause older adults to recruit the IFOF in a compensatory manner. The findings of this dissertational research both demonstrate the nuances of how VDR changes in aging and illustrate that there is still much more to be learned about this selective encoding process.

Appendix

<u>**Remember-Know-Guess Instructions (Adapted from Gardiner & Java, 1990)**</u>

Soon you will be shown a series of individual words and asked if you recognize the word from the studying phase or if it is a new word. For words you recognize, you will also be asked whether you recognized it due to remembering, knowing, or guessing. Now, I will describe what we mean by remembering and knowing:

Often, when *remembering* a previous event or occurrence, we consciously recollect and become aware of aspects of the previous *experience*. At other times, we simply *know* that something has occurred before, but without being able consciously to recollect anything about its occurrence or what we *experienced* at the time. For example, if seeing a hammer reminds you that you nailed up a picture frame a few days ago, and you can remember what it was like nailing up that picture, you would label that *remembering*. In contrast, if someone asks you what a hammer is, and you are certain you know what hammers are, but you can't remember any specific experiences with a hammer, you would call that *knowing*. The key distinction, again, is that in remembering you can recall a specific experience, whereas in knowing you cannot.

Before we go on, can you tell me what it means to remember given my earlier definition?

Today, remembering means that you consciously recall having seen the word previously in this study, and this can include any details related with that experience. This could be visual, such as being able to remember vividly what the word looks like. Also, if seeing the word earlier made you *think* of anything, and you can remember that on the recognition task, we will label that remembering. Now, please *only* give a remember response if you *are sure* that you have this conscious experience. In contrast, *knowing* means that you are certain you saw the word before,

but you are unable to consciously remember the experience. A third response, *guessing*, will

indicate that you are uncertain that you saw the word before.

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