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Neural Mechanisms of Value-Directed Remembering In Young and Older Adults

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Michael Stewart Cohen

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ABSTRACT OF THE DISSERTATION

Neural Mechanisms of Value-Directed Remembering in Young and Older Adults

by

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Doctor of Philosophy in Psychology

University of California, Los Angeles, 2015

Professor Barbara J. Knowlton, Co-Chair

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This dissertation examines how manipulation of value during encoding leads to better memory for high-value items. We use a variant of the value-directed remembering paradigm (Castel, Benjamin, Craik, & Watkins, 2002), a particular context for manipulating value at encoding that provides learners with the opportunity to metacognitively assess and strategically control encoding processes. Prior studies to investigate effects of value on memory have largely focused on how signaling from dopamine-producing reward regions directly facilitates formation of memories in the hippocampus. Such mechanisms seem to have little effect on memory here. Instead, our focus is on the cortically-mediated processes that learners can strategically engage to improve memory. In Chapter 2, we show that the degree of value-related modulation of brain activity in regions typically associated with semantic processing is critical, as selectivity with this brain mechanism correlates with how strongly value affects free recall in young adults. In Chapter 3, we show that a similar mechanism underlies selectivity in older adults. We also find evidence that young adults engage additional brain mechanisms that older adults do not, such as an increased proactive engagement of prefrontal cortex during the cue that precedes the to-be-remembered word when that cue is high-value. These additional mechanisms turn out to be largely ineffective. The fact that age-dependent mechanisms are not effective may relate to why older adults are successful at being selective in this paradigm. In chapter 4, we find that value can also modulate memory via increased deactivations in medial posterior brain regions, in both young and older adults. In addition, a set of behavioral studies applying a dual-process analysis to value-directed remembering shows that high-value items in this paradigm typically show increases in both recollection and familiarity relative to low-value items, consistent with selective application of deep encoding strategies. When the opportunity for free recall with feedback is removed, and, separately, in a subset of participants who report being insensitive to value, only recollection is enhanced, consistent with effects driven by more automatic, possibly dopamine-driven mechanisms, in response to reward.

The dissertation of Michael Stewart Cohen is approved.

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2015

DEDICATION

To my maternal grandparents, Shirley and the late George Alberstat, who have been an example to me of older adults who have remained mentally sharp and active well into old age, and who have been a vital support for me throughout my life.

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CHAPTER 1

Introduction and Overview

Introduction to Value-Directed Remembering

The ability to use memory effectively requires one to focus on more important to-be-remembered information at the expense of less important information. For example, while a great deal of information may be given out at a medical appointment, some of it may be vital for the patient to remember (e.g., the name of a new medication), while some may be less important (e.g., the patient's weight) and perhaps not even worth the effort to remember. Previous studies (e.g., Castel et al., 2002) have shown that both young and older adults are able to selectively remember words associated with more "points" compared to those associated with fewer "points" in order to maximize their point total at recall. In addition, although healthy older adults recall fewer items overall than young adults, they actually score higher than young adults on a measure of memory efficiency known as the selectivity index (Castel et al., 2002). This means that older adults tend to be closer to the optimal point total for the number of items that they recalled. It is also notable that the older adults tested by Castel et al. were just as likely to remember the highest-value items as young adults, even though they recalled fewer words overall. Thus, healthy older adults are able to successfully implement the strategies necessary to direct their limited cognitive resources towards remembering the most valuable items.

At the same time, it is important to note that the proficient use of value appears to be limited to healthy older adults, as older adults with even very mild dementia perform notably worse. Specifically, while Castel, Balota, and McCabe (2009) found that the selectivity index for healthy older adults in their sample tended to equal that for young adults, older adults in the earliest stage of Alzheimer's Disease displayed a significant reduction in selectivity index. Selectivity tended to be reduced even further for individuals with slightly more advanced (but still generally mild) Alzheimer's. In addition, working memory span tended to correlate positively with selectivity for both healthy older adults and those with mild dementia. Thus, it would appear that older adults' ability to be selective in memory encoding requires processing resources that are vulnerable to dementia and cognitive decline.

Other work examining the developmental trajectory of and the effect of cognitive dysfunction on the ability to selectively encode high-value stimuli provides some additional understanding of the processes involved in the selectivity paradigm. In a sample that included individuals from across the entire lifespan, Castel et al. (2011a) found that selectivity index changes across the lifespan in a very different way than total memory. Overall recall was best for college students and adolescents, with middle-age adults showing a significant decline in performance, and older adults and young children having the worst memory. By contrast, selectivity was consistently strong across young adults, middle-age adults, and young-older adults (ages 65-79). The oldest older adults (ages 80-96) did show some decline in selectivity, while children and adolescents had the lowest selectivity index. These data indicate that selectivity depends on aspects of cognition that mature relatively late, but that are maintained through nearly the entire remainder of the lifespan in healthy individuals.

Hanten et al. (2007) tested normally developing children from ages 6-18 in the selectivity task, and found a similar dissociation in developmental trajectory for total memory versus the selectivity index. Specifically, there was a significant quadratic component to the effect of age on number of items recalled, with sharper increases from age 6 to about age 13, but less of an increase across the adolescent portion of the sample. By contrast, selectivity index increased linearly with age. This result provides further evidence that memory selectivity depends on cognitive and/or neural processes that continue developing through adolescence. Castel, Lee, Humphries, and Moore (2011b) also tested 6-9 year old children with ADHD, and compared performance of those children on the selectivity task to that of normal children. While there were no significant effects of ADHD on the number of words recalled, children with the combined or hyperactive/impulsive ADHD subtype showed significant reductions in the selectivity index compared to both normal children and those with the inattentive ADHD subtype. These results again provide some indirect evidence as to the neural mechanisms of selectivity, suggesting that prefrontally-mediated planning abilities may be crucial.

Finally, it is worth noting that the findings from the selectivity paradigm have been extended to a more realistic context. Castel (2005) asked older adults to associate grocery prices with items, but included prices that were either realistic, overpriced, or underpriced compared to the actual value of the items. Older adults performed at least as well as young adults when recalling the realistic prices, but showed reduced recall performance for the specific unrealistic prices. They were, however, as good as or better than young adults at associating items with price categories (accurate, underpriced, or overpriced). Thus, older adults are able to remember the information that would be practically relevant for a shopping trip as well as do young adults, but they do not do so for information that would be irrelevant. These results imply that the cognitive processes used to enhance recall of valuable material in the laboratory selectivity paradigm are likely also used to produce adaptive behavior in a number of real-world contexts.

Overview of the dissertation

Prior studies, including those described above (e.g., Castel et al., 2009, 2011a, 2011b; Hanten et al., 2007), have done a good job elucidating the developmental trajectory of the pattern of results that was initially reported by Castel et al. (2002; see also Watkins & Bloom, 1999). Other studies have shown a number of different contexts to which those basic results can generalize (e.g., Castel, 2005; McGillivray & Castel, 2011). A recent study by Hayes, Kelly, and Smith (2013) showed that, when task demands are increased, by including items with negative values in the study list, older adults are not able to match young adults on selectivity, providing some information about the boundary conditions on older adults' ability to be successful in this task. Still, less is known about the broader neural and cognitive mechanisms that are called upon when people are performing this task.

A study by Ariel and Castel (2014) showed that pupillary dilation is greater for high-value than for low-value items, and they cite literature suggesting that this effect is unlikely to merely reflect increased emotional arousal; instead, it reflects selective deployment of attention to high-value items. This dissertation aims to provide a more detailed mechanistic explanation of what kinds of cognitive processes and neural systems people are engaging selectively during encoding high-value words. Doing so will help make deeper connections between the relatively specialized literature on value-directed remembering, and the larger literature on memory, cognitive control, and cognitive aging.

An initial study that I conducted (with Robert Bjork, Alan Castel, and Michael Friedman) to understand the mechanistic basis of the value-directed remembering paradigm involved varying the level of processing induced at encoding along with the point value associated with each item. One idea behind that paradigm was that, if people tended to encode high-value items using something like deep levels of processing, i.e., if the mechanistic basis for the two manipulations were similar, then the effect of varying the level of processing induced on a given item would be less for high-value items than for low-value items (cf., Chow, Currie, & Craik, 1978). Although initial evidence tentatively supporting such an explanation was reported in poster form (Cohen, Castel, Friedman, & Bjork, 2010), that study ultimately proved inconclusive. That experiment is not described in full here, and the experiments described in the present work use very different methods to address the question of what, mechanistically, underlies people's ability to selectively remember high-value items in the value-directed remembering task. Still, the present experiments ultimately converge on a similar answer as what we hypothesized at the outset of that effort: that the primary mechanism by which people selectively encode high-value items is in fact something analogous to deep levels of processing.

Chapter 2 represents our initial investigation of how brain activity during encoding differs for high-value items relative to low-value items in the value-directed remembering paradigm in young adults. The question of particular interest there was to determine the brain mechanisms by which the degree of differential activity at encoding, as measured by the difference in BOLD signal for high-value vs. low-value items, correlates with individual differences in how selective people are on the free recall test presented at the end of each list. We can assume that regions showing such an effect are the ones in which modulation of brain activity by value is consequential for later memory success.

In Chapter 3, we extend our findings to older adults, looking for similarities as well as differences between age groups in the brain mechanisms by which high-value items are more successfully encoded. We specifically look for age-related differences in the spatial distribution, and in the timing relative to events within the trial, of activations underlying memory selectivity. These data are particularly relevant given previous findings that healthy older adults are able to be as selective as young adults in this paradigm. Thus, we can assume that mechanisms that are similarly activated, and similarly related to behavior, across both age groups show relative preservation of functionality with aging. In addition, if we were to find regions in which brain activity correlates with performance in older adults but not in young adults, such activity could be informative regarding the neural mechanisms of compensation (c.f., Cabeza, 2002; Rajah & D'Esposito, 2005).

Finally, in Chapter 4, we explore how encoding in the value-directed remembering paradigm separately affects recollection and familiarity components of memory (Yonelinas, 2002). The MRI datasets described in Chapters 2 and 3 both included a post-scan recognition test administered at a longer temporal delay than the primary free recall tests. From this test, we can estimate relative contributions of recollection and familiarity using a receiver operating characteristics (ROC) analysis. In Experiment 1A (young adults) and 1B (older adults) of Chapter 4, we examine correlations between value-related differences in brain activity during the encoding task and value-related differences in ROC process estimates. While this analysis is likely to overlap some with the findings reported in Chapters 2 and 3, we also expected that it might show additional brain mechanisms by which value-related modulation at encoding affects underlying memory strength beyond those that affect free recall.

On a behavioral level, Experiment 1A of Chapter 4 was somewhat inconclusive as to whether value-directed remembering enhances only recollection, or whether it enhances both recollection and familiarity. This distinction is important, given evidence that encoding manipulations that affect explicit encoding processes, such as the use of deep vs. shallow levels of processing, tend to increase both recollection and familiarity (Yonelinas, 2002), while manipulations of reward that are assumed to operate on a more automatic level are associated with increased recollection, but generally do not increase familiarity (e.g., Shigemune, Tsukiura, Kambara, & Kawashima, 2014; Wittman, Dolan, & Düzel, 2011, Exp. 1). Thus, Chapter 4 also includes a set of behavioral studies run on young adults, intended to more fully probe how value affects recollection and familiarity.

In Experiments 2, 4, and 5 of Chapter 4, we examined the dual process correlates of a relatively standard version of the value directed remembering paradigm. We dissociated contributions of the two processes in memory for high-value and low-value items using multiple methods: Remember/Know judgments in Experiment 2, while in Experiments 4 and 5, we required memory for source information on the free recall test, and also gave forced-choice recognition tests that were intended to rely on one process or the other. In Experiments 3 and 6, we examined how the use of multiple study-test cycles in the value-directed remembering paradigm affects value-related modulation of encoding processes. Specifically, we took out the free recall tests, instead telling participants to prepare for a later recognition test. Again, we used multiple methods to dissociate the two processes, using Remember/Know judgments in Experiment 3, and process-specific recognition tests in Experiment 6. We could then determine how value affects the dual process correlates of memory in this modified value-directed remembering paradigm, compared to what we observe in the more standard versions used in Experiments 2, 4, and 5.

CHAPTER 2

Value-based modulation of memory encoding involves strategic engagement of fronto-temporal semantic processing regions[1]

It is generally true that some of what a person encounters is important to remember, while other things are less important. One critical operation is to selectively remember important information, often at the expense of less important information. For instance, when studying for an exam, some students might maximize efficiency, focusing exclusively on the most important material. Other students might not be as selective; even though they know that some items are more important than others, they may still try to remember as much as possible, a strategy that often leads to poorer results. The present work uses fMRI to better understand what people do differently, on both a cognitive and neural level, when remembering items deemed important.

In order to address these questions, we used a variant of the value-directed remembering (VDR) paradigm (Castel, Benjamin, Craik, & Watkins, 2002; Castel, 2008). The VDR paradigm involves having participants study a list of words paired with point values, with the participants' goal being to maximize the total score, which is the sum of the

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[1] This chapter is adapted from:
Cohen, M.S., Rissman, J., Suthana, N.A., Castel, A.D., & Knowlton, B.J. (2014). Value-based modulation of memory encoding involves strategic engagement of fronto-temporal semantic processing regions. *Cognitive, Affective, and Behavioral Neuroscience, 14,* 578-592.

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values associated with recalled words. A number of behavioral studies (e.g., Ariel & Castel, 2014; Castel et al., 2002; Castel, Farb, & Craik, 2007; Castel, Murayama, Friedman, McGillivray, & Link, 2013; Hanten et al., 2007; Loftus & Wickens, 1970; Soderstrom & McCabe, 2011; Watkins & Bloom, 1999) have shown that words that are arbitrarily determined to be valuable (via high point values) tend to be recalled better than words that are arbitrarily assigned lower values. However, prior studies with this paradigm have been limited in fully explaining the effect on a mechanistic level, with explanations ranging from differential forms of rehearsal, use of imagery, and strategic encoding and retrieval operations.

There is reason to believe that people are making an explicit effort to prioritize encoding of high-value items in the VDR paradigm. Specifically, the degree to which people optimize their point score, as measured by the *selectivity index* (Castel et al., 2002), increases from earlier lists to later lists (Castel, 2008; Castel et al., 2011a). The VDR paradigm is structured such that people learn multiple distinct word lists, with a free recall test after each list and immediate feedback on the number of points earned after each test. The improvement in selectivity across lists suggests that people may be learning about how many words they can remember and about which encoding strategies will lead to the highest point total. This pattern of results would be consistent with the use of explicit cognitive strategies to enhance encoding of high-value items.

A number of functional neuroimaging studies have examined the brain mechanisms that might mediate the enhancement of memory for high-value items. Adcock, Thangavel, Whitfield-Gabrieli, Knutson, and Gabrieli (2006) were the first to do so in the context of an intentional encoding paradigm. They found that increased activity in regions of the dopaminergic reward system, specifically the ventral tegmental area (VTA) in the midbrain and nucleus accumbens (NAcc) in the ventral striatum, elicited in response to a value cue that preceded presentation of the actual stimulus, predicted successful encoding of high-value items. A similar pattern was observed in the hippocampus, and moreover the functional connectivity between VTA and hippocampus was strongest during cues preceding high-value items that were subsequently remembered. These findings suggest that input from the midbrain reward system might serve to prepare the hippocampus to better encode the important information that is about to be encountered, in this case a photograph of a landscape scene. Such connections between dopaminergic midbrain systems and the hippocampus had previously been shown to be important in rodents (Huang & Kandel, 1995; Jay, 2003; Lisman & Grace, 2005), but this was the first direct evidence for such a mechanism in humans.   While the study by Adcock et al. (2006), and subsequent work by others (e.g., Murty, Labar, and Adcock, 2012; Wolosin, Zeithamova, and Preston, 2012) have contributed valuable insights about the neural mechanisms that can underlie reward-based learning, there are likely to be additional mechanisms whereby people strategically process high value items differentially to optimize limited memory. We focus primarily on those mechanisms in the present paper.

One difference between selective strategic enhancement of memory for valuable items and midbrain reward-motivated learning mechanisms is the time course of these effects. For example, Adcock et al. (2006) tested memory at a delay of 24 hours, following evidence from rodent work (e.g., O'Carroll, Martin, Sandin, Frenguelli, & Morris, 2006; Frey, Schroeder, & Matthies, 1990; Frey, Matthies, Reymann, & Matthies, 1991) suggesting that enhancement of encoding for valuable items via dopamine-driven increases in hippocampal plasticity is likely to emerge only after a delay. Although Adcock et al.'s study did not include an immediate memory test for comparison, Spaniol, Schain, and Bowen (2014) tested young and older adults on a very similar task and found that on an immediate test, value did not reliably enhance memory in either age group. With a test given 24 hours after encoding, however, they replicated the finding of a significant enhancement of memory for valuable items. Similarly, Murayama and Kuhbandner (2011) found that after a 1-week delay, monetary rewards increased memory for trivia questions that were not inherently interesting, an effect believed to be dopamine-driven. No effect of reward on memory was observed on an immediate test, however, again suggesting that effects of the putative dopaminergic reward-motivated learning mechanism that Adcock et al. and others have examined only emerge after a delay. Reward-related activity in the VTA-hippocampal circuit thus appears to engage a consolidation process that makes memory for valuable items less vulnerable to forgetting after a delay, but this process does not seem to affect retrievability in the shorter term. However, under different circumstances, people can improve their memory for valuable items in a way that is apparent in tests administered immediately following learning (e.g., Castel et al., 2002; Castel, 2008). It thus seems likely that there is an additional mechanism capable of enhancing the encoding of valuable items that is engaged by the VDR paradigm, and most likely by certain real-world situations as well.

As noted above, there is reason to believe that participants in the VDR paradigm gradually learn to employ effective mnemonic strategies that allow them to strengthen encoding of high-value items; this is apparent both from the pattern of recall data across lists and from post-experiment self-reports (e.g., Castel, 2008; Castel, McGillivray, &

Friedman, 2012). In contrast, participants in most studies of reward-motivated learning (e.g., Adcock et al., 2006) are presented with a long list of stimuli, and memory is only tested after all encoding is complete with no opportunity to modify encoding strategy based on feedback. Additionally, performance in the VDR paradigm is typically assessed via free recall, whereas memory in reward-based learning tasks is usually assessed by a yes/no recognition task. Thus, the VDR task is more likely to tap into strategic enhancement of encoding for high-value items than are paradigms that are typically used to assess reward-based learning. Additional neural mechanisms may be engaged during encoding of high-value items in the VDR paradigm that may reflect real-life situations in which people are able to preferentially remember valuable information.

To our knowledge, no prior neuroimaging studies have examined effects of value on neural mechanisms of strategy use during encoding of items with different values. However, a number of studies have examined which brain areas are preferentially recruited when people engage in deep encoding of study materials versus shallower encoding. One of the first such studies (Kapur et al., 1994) examined how tasks structured to promote different levels of processing (Craik & Lockhart, 1972; Craik & Tulving, 1975) differentially affected cerebral blood flow. They found that a task that engaged deep encoding by evoking semantic representation of words was associated with greater activity in the left inferior prefrontal cortex (PFC), relative to a task that required only surface-level encoding. Thompson-Schill, D'Esposito, Aguirre, and Farah (1997) provided a more precise account of left inferior PFC function, suggesting that the role of this region is specifically in the selection of the most relevant semantic representation(s) for a given task, rather than in the retrieval of semantic knowledge more generally. Subsequent studies (e.g., Wagner et al., 2001; Badre et al., 2005) have further clarified how left inferior PFC contributes to controlled semantic processing; see also reviews by Bookheimer (2002), Costafreda et al. (2006), and Badre & Wagner (2007).

Other work has more directly implicated left PFC in the use of verbal or semantic strategies at encoding. When participants are instructed to use a semantic clustering strategy, they tend to show increased activity in areas including left dorsolateral and left ventrolateral PFC at encoding, relative to earlier blocks when such a strategy is possible but has not been explicitly instructed (Savage et al., 2001; Miotto et al., 2006). Similarly, Kirchhoff and Buckner (2006) showed that individual differences in encoding-related activity in left inferior PFC are associated with the degree to which people report having used a verbal elaboration strategy during encoding. Use of these elaborative strategies was associated with better memory performance, suggesting that the often-observed association between left ventrolateral prefrontal activity at encoding and successful subsequent memory (e.g., Wagner et al., 1998; Kim, 2011) is mediated by increased use of semantic strategies at encoding. One possible neural mechanism underlying enhanced memory for high-value items in the VDR paradigm may be the differential engagement of regions associated with the use of semantic strategies at encoding. Such a finding would be particularly interesting given that prior work has largely ignored the ways in which intentional strategic processing can mediate the effects of value on memory.

Method

Participants

Twenty-two young adults participated in the study. Data from two participants were excluded, one for being a non-native English speaker, and a second who was only able to complete 3 lists due to discomfort in the scanner. The remaining twenty participants (mean age = 21.65, SD = 3.66, age range = 18-30; 11 female, 9 male) were all right-handed, native English speakers who reported no current psychoactive medications or severe psychiatric or neurological disorders. All participants either had normal or corrected-to-normal vision. Written consent was obtained from each participant, and all procedures were approved by UCLA's Medical Institutional Review Board. Participants were recruited via flyers posted on the UCLA campus, and were paid $10/hour, plus additional earnings from the Monetary Incentive Delay (MID) task (typically $10-$12), and also had the chance to win up to an additional $25 in a delay-discounting task (Kirby, Petry, & Bickel, 1999) that we ran after the scan. For one participant, we were unable to finish data collection on one run of the VDR task due to discomfort, but the remaining four VDR runs for that participant are included in our analyses.

Task Stimuli and Behavioral Procedures

Our VDR task paradigm was based on that used by Castel et al. (2002), but was altered to make it more amenable to neuroimaging (see Figure 2.1). Each trial of our task began with a cue for point value, either high-value (10, 11, or 12 points) or low-value (1, 2, or 3 points), presented as a number inside of a gold "coin" on the screen for 2 s. This was followed by a fixation cross of jittered duration (equal proportions 3 s, 4.25 s, 5.5 s, and 6.75 s). Next, a word was presented for 3.5 s, followed by 1.5 s of fixation and then an active baseline task (Stark & Squire, 2001) of jittered duration (50% 4 s, 25% 6.5 s, 25% 8 s). The vowel-consonant baseline task involved the presentation of a pseudorandom series of letters, with an approximately equal ratio of vowels and consonants. Each letter was presented for 1 s, with a 0.25 s fixation between letters, and a 1.5 s blank screen at the end

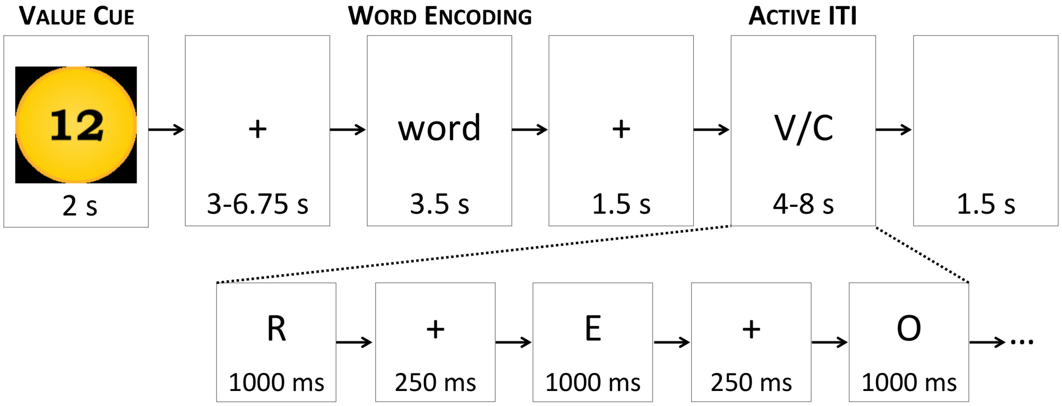

Figure 2.1. Value-directed remembering task design. On each trial, participants are first presented with the value cue, then with a to-be-remembered word, and finally with a 2-6 trials of an active baseline task (vowel/consonant judgment) to be performed during the inter-trial interval (ITI).

of the trial. Participants were instructed to respond to each letter while it was still on the screen. Button mappings were fixed across subjects, such that all individuals used their index finger if the letter was a consonant and their middle finger if the letter was a vowel. Letters in the vowel-consonant task were arranged such that they did not spell any words. We used a vowel-consonant task in order to continually engage verbal processing resources throughout the inter-trial intervals, thereby reducing our participants' ability to simultaneously engage in verbal rehearsal of the words during this time.

Each list included 24 different words, of which 12 were arbitrarily defined as high-value and 12 arbitrarily defined as low-value (with 4 words at each specific value level). Five lists of the VDR task were presented in the scanner. Items were drawn from clusters 6 and 7 of the Toglia and Battig (1978/2009) "Colorado" word norms. All stimuli were 4-8 letter, 1-2 syllable nouns, rated as highly familiar (range 5.5-7 on a 1-7 scale), moderate to high on concreteness and imagery (range 4-6.5 on a 1-7 scale), and moderate in pleasantness (range 2.5-5.5 on a 1-7 scale). Values were pseudorandomly assigned to words, with the assignment of particular words to value group (high or low) counterbalanced across subjects. The order in which the different lists were presented in the scanner was also counterbalanced. Each list began with 12.5 s of fixation and ended with an extra 15 s of the vowel-consonant task. Within about 10- 20 s after the end of each scan, the recall test began, and the participant was given 90 s to recall as many words as possible from the preceding list. Immediately after recall was complete, the experimenter scored the test, and gave feedback on the point score earned for that list.

Prior to scanning, participants were given detailed instructions about the VDR task, and then completed six practice items, followed by two full practice lists. Each of the two full practice lists included recall tests with feedback. Prior work has shown that selectivity is typically stronger on the third and subsequent lists than on the first two lists (Ariel & Castel, 2014; Castel, 2008; McGillivray & Castel, 2011). Thus, we assumed that by presenting two full lists prior to scanning, strategy use would be relatively well established and consistent in the scanner.

After completion of the VDR task, participants remained in the scanner to perform one run of the MID task (Knutson, Adams, Fong, and Hommer, 2001), which was intended to serve as a functional localizer task for the VTA and NAcc. This task included a total of 48 trials, equally divided into high-reward (+$1.00), low-reward (+$0.10), and no-reward (+$0.00). Loss/punishment trials were not included, as these were not relevant for our purposes. In addition, our version of the task includes feedback in word form, unlike the symbolic cues used in the classic MID paradigm, but consistent with the version used by Samanez-Larkin et al. (2007). This version is intended to be more amenable for use with older adult participants. While the number of trials of each type may appear low, a recent study by Wu, Samanez-Larkin, Katovich, & Knutson (2014) used a similar number of trials of each type and reported robust and consistent changes in BOLD signal as a function of value.

Each trial began with a text cue indicating the potential value of that trial (e.g., "Win $1.00"). To earn this reward, the participant was required to make a button-press during the brief window of time that a square stimulus appeared on the screen. As in prior studies with this paradigm, we used an adaptive algorithm, which adjusted the response period to keep the overall win percentage at approximately 66%. The initial response period for the practice run outside the scanner was 300 ms, and the initial response period in the scanner was determined based on the average response time for successful responses during practice. If the participant's win percentage exceeded 66%, the response period would tend to be made shorter (i.e., more difficult) on the next trial. If the participant's win percentage was less than 66%, the response period would tend to be made longer (i.e., easier) on the next trial, down to a minimum possible response period of 140 ms. Overall, mean accuracy across the 18 participants for whom we have behavioral data, was 60.4% (SD = 8.3%) for $0.00 trials, 60.4% (SD = 7.1%) for $0.10 trials, and 60.1% (SD = 6.5%) for $1.00 trials. Mean RTs for correct trials were 195.8 ms (SD = 27.3 ms) for $0.00 trials, 178.6 ms (SD = 29.3 ms) for $0.10 trials, and 169.9 ms (SD = 26.9 ms) for $1.00 trials.

The experimental session also included several supplementary behavioral measures before and after scanning. Prior to scanning, we ran reading span and counting span tests (Kane et al., 2004) to measure working memory capacity. We used a partial-credit load-weighted scoring procedure such that each unit that was correctly recalled, in the correct serial position, was scored as 1 point (Conway et al., 2005). Following guidance by Conway et al. (2005), we generated a composite measure of working memory from scores on these two tests. Because we did not have enough data to do a true latent variable analysis, we computed z scores for each measure, and averaged the z scores to yield a composite measure of working memory.

At the end of the session, we administered a debriefing questionnaire that included questions about what strategies participants had used to encode the words, what (if anything) they had done differently during encoding of the high-value words, and questions about what (if anything) they were rehearsing during the fixation and vowel-consonant periods. Self-reported encoding strategies were categorized as either relying upon semantic aspects of the words, or as relying more on surface features of the words. We also classified each participant into one of 3 categories: only attempting to encode high-value items (ignoring low-value items), trying harder on high-value items, or ignoring value entirely. We also categorized self-reported encoding strategies as either relying upon semantic aspects of the words, or as relying more on surface features of the words.

Scanning Procedure

T2*-weighted echoplanar (EPI) images sensitive to blood oxygenation level dependent (BOLD) contrast were collected using a 3 T Siemens Tim Trio MRI scanner at the UCLA Staglin IMHRO Center for Cognitive Neuroscience. For the VDR task, each 179-volume functional run lasted approximately 7.5 min; five such runs were acquired for each participant. Each functional volume consisted of 45 interleaved axial slices, TR = 2500 ms, TE = 25 ms, flip angle = 75°, slice thickness = 3.0 mm, in-plane resolution = 3.0 x 3.0 mm, matrix = 64 x 64, FOV = 192 mm, and no gap between slices. For the MID task, similar scan parameters were used, except that the TR was shortened to 2 s, only 36 slices were acquired per volume, and only one 246-volume run was collected. In addition, we collected matched-bandwidth T2-weighted coplanar structural scans to use as an intermediate step in spatial registration. We also collected a high-resolution structural scan (MPRAGE), using the following parameters: TR = 1900 ms, TE = 3.26 ms, flip angle = 9°, 176 slices, 1 mm^3 voxels, 18.2% slice oversampling, FOV = 250 mm, with GRAPPA acceleration. To minimize head movement during scanning, we placed extra cushions between the subject's head and the coil. Stimuli were presented using E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA), and images were shown via either a custom-built MR-compatible rear projection system, or via MR-compatible goggles (Resonance Technology, Inc.).

fMRI Data Analysis

Preprocessing. Analyses of EPI data were carried out using FEAT v5.98 (fMRI Expert Analysis Tool), as implemented in FSL v4.1.9 (www.fmrib.ox.ac.uk/fsl). We corrected for head motion using MCFLIRT (FMRIB's motion correction linear image registration tool; Jenkinson et al., 2002), and also used the fsl_motion_outliers script to detect and censor any volumes with excessive head motion. We then removed non-brain tissue using BET (Brain Extraction Tool; Smith, 2002). Grand-mean intensity normalization was applied to the 4D dataset from each run based on a multiplicative scaling factor. We applied a Gaussian kernel of 5 mm FWHM for spatial smoothing, and for temporal filtering, a high-pass filter to remove low-frequency noise using a Gaussian-weighted least-squares straight-line fitting with a sigma of 100 s. Temporal autocorrelation was corrected for using prewhitening as implemented by FILM (FMRIB's improved linear model; Woolrich et al., 2001). Functional images were registered to a coplanar structural scan and then to a high-resolution structural scan using FLIRT (FMRIB's Linear Image Registration Tool) linear registration. Registration from the high-resolution structural scan to standard Montreal

Neurological Institute (MNI) space was further refined using FNIRT (FMRIB's Non-linear Image Registration Tool).

Analysis of Value-Directed Remembering Task. We included four different event types in the statistical model: high-value cue period, high-value word-encoding period, low-value cue period, and low-value word-encoding period. The cue period was defined based on the time period in which each value cue was on-screen, 2 s in duration, convolved with a double-gamma hemodynamic response function (HRF). The word-encoding period was defined as a separate event, based on the time period in which the to-be-learned word was on-screen, 3.5 s in duration, convolved with a double-gamma HRF. Temporal derivatives were included in the model for all four event types. Motion regressors generated by MCFLIRT and regressors coding for any motion outlier TRs were also included in the model as covariates of no interest.

First-level general linear model (GLM) analysis was carried out separately for each run. Then, in a second-level fixed-effects analysis, we combined the parameter estimates across all five runs of the VDR task, and created a set of linear contrasts. Our primary contrasts of interest compared the BOLD signal during high-value vs. low-value items, looking separately at the cue period data and the word-encoding period data. For whole-brain analyses across subjects, we used the FLAME stages 1 and 2 mixed effects model in FSL, with automatic outlier detection. Clusters were determined using a voxel-level threshold of $Z > 2.3$, with a cluster-corrected significance level of $p < .05$.[2] Cortical surface renderings were created using Caret v5.65 (http://brainvis.wustl.edu; Van Essen et al.,

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[2] Instead of using a more stringent threshold, we felt that it was preferable to present a more complete picture of activity represented in a given contrast, while also employing dynamic range in the figures to highlight the regions that would emerge with a stronger threshold.

2001) on the inflated Conte69 atlas in FNIRT space (Van Essen, Glasser, Dierker, Harwell, and Coalson, 2012), with FSL activation maps transformed from volume to surface space using Caret's interpolated voxel algorithm. Activation peaks noted in the tables were a subset of the local maxima generated for each contrast by FSL's "cluster" command, with a minimum distance of 10 mm between peaks. Labels were determined using the Harvard-Oxford structural atlas and other relevant brain maps (e.g., Talairach & Tournoux, 1988; Brodmann, 1909), and redundant peaks were eliminated.

We computed each participant's *selectivity index* for each list using the formula [(actual score – chance score) / (ideal score – chance score)], as described in prior literature (Castel et al., 2002; Watkins & Bloom, 1999). We then averaged the selectivity indices across all scanned lists to yield a single score. To search the whole brain for correlations between behavioral measures (e.g., selectivity index) and changes in BOLD signal, we included the behavioral measure as an EV in an FSL group-level model, in addition to the group mean. For region of interest (ROI) analyses, we computed Pearson correlation coefficients across participants using each individual's mean selectivity index and the mean parameter estimates for a given contrast in a given ROI for each participant. We applied a Bonferroni-Holm correction (Holm, 1979) to correct for multiple comparisons across each set of related ROIs; unless otherwise indicated, all effects survived this correction for the particular cohort of ROIs tested.

Analysis of Monetary Incentive Delay Task. The analysis workflow applied to MID task data was generally similar to that described for the VDR task. We modeled the cue period and the feedback period as separate event types, each convolved with a double-gamma HRF. The cue period was defined as an event of 2 s duration during which the value cue was on-screen. The feedback period was defined as an event of 1.92 s duration during which feedback (i.e., whether or not the participant had "won" on a given trial) was on-screen. High-value, low-value, and no-reward trials were defined as separate event types. Our primary analysis of interest compared activity during the cue period on high-value trials with activity during the cue period on no-reward trials. Group level analyses followed the same procedure as described for the VDR task.

Results

Behavioral data

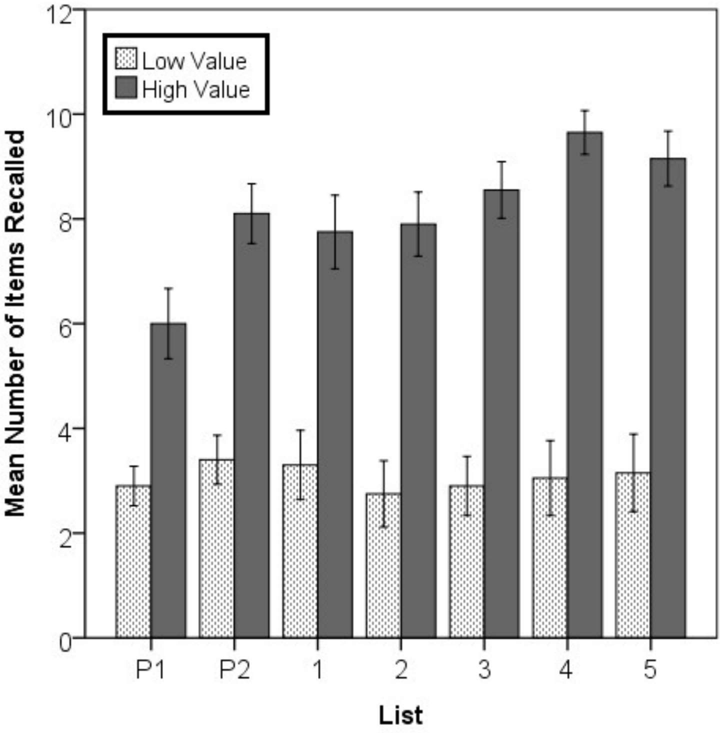


Figure 2.2. Mean number of high-value and low-value items recalled on each list in young adults (including on the two practice lists shown prior to scanning). Significantly more high-value items were recalled than low-value items on all lists. Error bars represent +/- 1 SE.

We first examined the behavioral data to confirm that high-value words were consistently recalled better than low-value words (Figure 2.2). Using paired-samples *t*-tests (two-tailed), we found that high-value words were remembered better than low-value words even on the first practice list, $t(19) = 4.13$, $p = .001$, and on the second practice list, $t(19) = 7.02$, $p < .001$. For the five lists presented in the scanner, a paired-samples *t*-test (performed on the data from the 19 subjects who completed all five lists) confirmed that the mean number of items recalled across all five scanned lists was significantly greater for high-value words, $t(19) = 9.58$, $p < .001$. A 2 x 5 (value-group x list) repeated-measures ANOVA on the proportion of items recalled additionally showed an interaction between list and value-group, $F(4, 72) = 3.15$, $MSE = 1.96$, $p = .019$, $\eta_p^2 = .149$, but no main effect of list, $F(4, 72) = 1.79$, $\eta_p^2 = .090$. The significant interaction suggests that point values had a reliably stronger effect on recall on later lists. Separate paired-samples t-tests for each list confirmed that there was still a highly reliable effect of value on all five scanned lists, with all *t*s > 6.00, and all *p*s < .001.

In addition, we examined data for the individual value levels, in part to confirm that the binarization into high vs. low value that we generally use throughout the dissertation is justified by the data (Table 2.1). For low-value items, a one-way within-subjects ANOVA did not find a difference in the number of items recalled across the three low-value conditions, $F(2, 38) < 1$, $\eta_p^2 = .004$. Within high-value conditions, a one-way repeated measures ANOVA showed a trend towards an effect of point value, $F(2, 38) = 2.97$, $MSE = 1.16$, $p = .063$, $\eta_p^2 = .135$. Significantly more 12-point items ($M = 9.17$) were recalled than 11-point items ($M = 8.50$), $t(19) = 2.83$, p = .028, but the difference between 11-point and 10-point items (M = 8.42) was not significant, $t(19) < 1$.

Table 2.1. Mean (SE) number of items recalled per list across the 5 scanned lists by specific point value in young adults.

Low Value			High Value		
1	2	3	10	11	12
0.99 (0.19)	1.03 (0.20)	1.01 (0.20)	2.81 (0.16)	2.83 (0.14)	3.06 (0.12)

Main effects of value

Cue Period. We first examine how brain activity differs during high-value trials as compared to low-value trials across individuals, during the cue period. A whole-brain analysis revealed several frontoparietal regions that showed greater BOLD signal in response to high value compared to low value cues (Figure 2.3A; Appendix A—Table A.1). In addition, as predicted, we observed significant effects in mesolimbic reward structures, including clusters in left nucleus accumbens (NAcc; peak voxel MNI coordinates: -6, 8, -4), and in right NAcc (peak voxel: 8, 10, -6). The whole-brain analysis also revealed a cluster in right pregenual cingulate cortex (peak voxel: 4, 44, 24), an area that has been associated with reward processing in a recent meta-analysis (Liu, Hairston, Schrier, & Fan, 2011). This cluster is immediately dorsal to the ventromedial prefrontal cortex, which is widely considered to be important in reward processing (e.g., O'Doherty, 2013).

In addition, we conducted ROI analyses to probe for differential levels of activity in

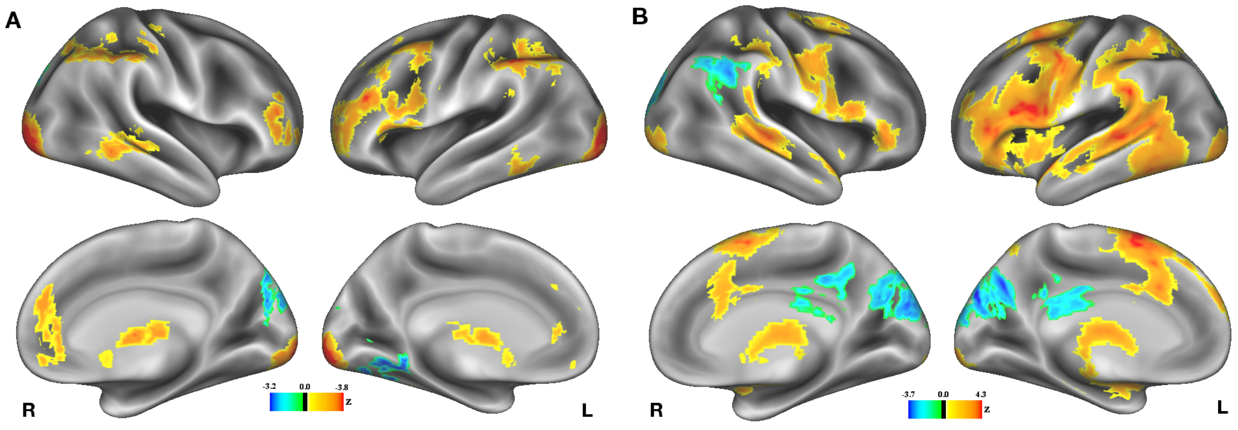


Figure 2.3. Group activation contrast showing main effects of value on BOLD signal (A) during the cue period, and (B) during the word encoding period. Warm colors indicate regions showing greater activity on high value trials, and cool colors indicate regions showing greater activity on low value trials. Note that scales were chosen separately for each contrast, and for positive and negative activations within each contrast, to maximize dynamic range, but the actual thresholds were constant across this and all other figures.

those specific reward-sensitive regions for which we had a priori hypotheses, specifically, VTA/midbrain and nucleus accumbens (NAcc)/ventral striatum. Our primary method of localizing these reward-sensitive regions was to locate the peak coordinates in midbrain and ventral striatum from a group-level analysis of the MID task. To localize the reward-sensitive midbrain, we placed a sphere of radius 4 mm around the peak midbrain coordinate obtained from the MID functional localizer task (L hemisphere: -6, -24, -6; R hemisphere: 6, -26, -6). We also functionally defined a NAcc/ventral striatal reward-sensitive region by placing a sphere of radius 4 mm around the peak coordinates in the vicinity of NAcc from the MID task (L hemisphere: -8, 12, -2; R hemisphere: 8, 10, -2). Because effects of value were reliably correlated across corresponding regions in the two hemispheres, and in order to increase statistical power, we combined L and R hemisphere spheres to create bilateral functionally-defined ROI for the NAcc and the midbrain. We found a significant effect of value in the bilateral NAcc/ventral striatum, $t(19) = 3.73$, $p = .001$. We also found greater activity during high-value cues in the reward-sensitive midbrain, $t(19) = 2.48$, $p = .022$.

Because our functionally-defined midbrain ROI is somewhat lateral, posterior, and superior to the typical anatomical definition of the VTA, possibly due to imperfect registration of midbrain BOLD signal to the anatomical template brain (e.g., Limbrick-Oldfield et al., 2012), we elected to also interrogate our data using an alternative VTA ROI, defined based on a probabilistic anatomical MRI atlas (Murty & Adcock, 2014; Shermohammed et al., 2012); we included all voxels that had non-zero probability values, resulting in a cluster of 698 voxels. Note that unlike our functionally-defined ROIs, which we defined separately in each hemisphere, this VTA ROI consists of a single midline region.

Within the anatomically-defined VTA ROI, activity tended to be greater during high-value cues than during low-value cues; this difference approached, but did not reach, significance, $t(19) = 1.84$, $p = .08$. Thus, it seems that there was generally more activity in reward-sensitive brain regions during high-value cues, relative to low-value cues.

Word-encoding period. We also examined differences in brain activity as a function of value during the word-encoding period (Figure 2.3B; Appendix A—Table A.2). A whole-brain analysis revealed greater BOLD signal during high-value encoding in a large cluster that included almost the entirety of the left inferior frontal gyrus (LIFG), including both the pars triangularis (peak voxel: -44, 32, 6), and the pars opercularis (peak voxel: -42, 8, 18). Whole brain analysis also showed greater activity during high-value encoding in the left superior temporal gyrus, and throughout the posterior portion of the left lateral temporal cortex (peak voxel: -46, -52, -12). Similar patterns of brain activity are apparent in homologous right-hemisphere regions, but these effects were weaker and less extensive than their left-hemisphere counterparts. In addition, during encoding of high-value words, there was less activity in bilateral posterior cingulate cortex and in right angular gyrus, suggesting greater deactivation of the default mode network during encoding of these items, relative to low-value words.

We also observe increased activity in dopaminergic striatal and midbrain regions during the word-encoding period for high-value words. Whole-brain analysis revealed clusters centered in the caudate/putamen bilaterally (L peak voxel: -16, 10, 10; R peak voxel: 22, 6, -8). In addition, we examined how value affected activity in NAcc/ventral striatal and midbrain reward-sensitive regions during word encoding using the same ROIs described above. We find significantly greater activity during high-value encoding in bilateral NAcc/ventral striatum, $t(19) = 4.23$, $p < .001$. We also find a significant effect of value in our reward-sensitive midbrain ROI, $t(19) = 3.02$, $p = .007$. Finally, we find a significant effect of value in our anatomically-defined VTA ROI, $t(19) = 2.26$, p = .036. Overall, we can conclude that these reward-sensitive brain regions were generally more active on high-value items, during the word-encoding period as well as during the cue period.

Correlation with Selectivity Index

Our primary question of interest concerns how value contributes to subsequent recall. Because many of the participants remembered few low-value words or forgot few high value words, it was not possible to construct a viable contrast representing the interaction between value and recall. We instead used an individual differences approach to examine the relationship between item value and memory success. Specifically, we correlated each individual's mean selectivity index with effects of value in the brain (i.e., the difference between activity on high value and low value trials in each voxel). Selectivity index reflects how close participants were to achieving an optimal point score, independent of the actual number of items recalled. We can thus infer that participants who were more selective in the words that they remembered on the recall test were engaging more strongly the processes that yield relatively better memory for high-value items in this task.

We first looked for regions in which the effect of value on BOLD signal during the cue period correlates with selectivity index. Whole-brain analysis yielded no significant correlations with selectivity index during the cue period. When using a whole-brain analysis to examine brain activity during the word-encoding period, however, a number of significant clusters emerged (Figure 2.4; Appendix A—Table A.3). Most notably, we found a correlation between selectivity index and value-related activity in a cluster that included the anterior portion of the left IFG and ventral portions of the left middle frontal gyrus (peak voxel: -46, 20, -6), and in a second cluster that included the left posterior IFG (peak voxel: -38, 6, 28). Another notable cluster is apparent in the posterior portion of the middle and inferior temporal gyri (peak voxel: -52, -64, -2).

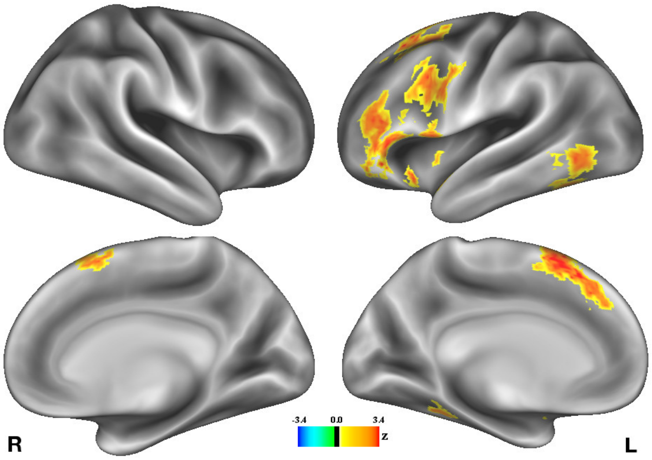
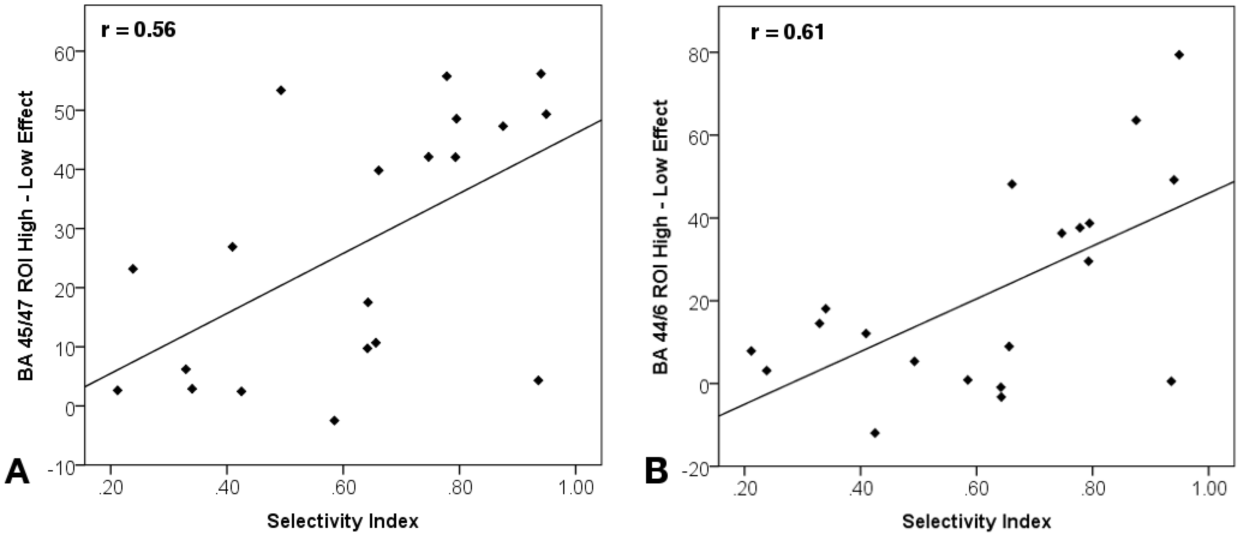


Figure 2.4. Map depicting regions demonstrating a significant positive correlation between selectivity index and effects of value on BOLD signal during the word encoding period. No regions demonstrated a significant negative correlation between these variables.

We also examined how selectivity index correlated with value-related changes in activity in the mesolimbic dopamine system. During the cue period, none of the three reward-sensitive ROIs described above showed significant correlations with selectivity index (NAcc: r = -.01, functionally-defined midbrain: r = -.27, anatomical VTA: r = -.11). During the word-encoding period, however, we found a positive correlation between selectivity index and value-related activity in nucleus accumbens/ventral striatum (r = .495, p = .026). After applying a Bonferroni-Holm correction, the corrected p value for this correlation is .052, narrowly missing our cut-off for significance; we nonetheless believe this trend is noteworthy. We did not find a correlation in our functionally-defined midbrain ROI (r = .12) during the word encoding period, but we do find a positive correlation between selectivity index and value-related in the anatomically-defined VTA ROI (r = .534, p = .015), and this correlation does survive a Bonferroni-Holm correction. Thus, while it seems clear that effects of value on activity in dopaminergic reward regions during the cue period do not positively correlate with memory selectivity, activation of dopaminergic reward regions during word encoding may make some contribution to greater selectivity.

To provide additional evidence for inferences about the use of cognitive strategies at encoding, we also examined value effects in three different a priori regions from a prior fMRI study of strategy use during encoding (Kirchhoff & Buckner, 2006). The three relevant peaks were in left anterior IFG (BA 45/47), left posterior IFG (BA 44/6), and extrastriate cortex (BA 19/37). Kirchhoff and Buckner found that activity in both IFG clusters correlated positively with use of verbal elaboration strategies during encoding. Activity in the extrastriate cortex correlated instead with the use of a visual inspection strategy, which would likely not be useful for our verbal materials. Thus, if participants were using elaborative verbal encoding strategies to selectively remember the high-value words in our study, we would expect to find correlations between selectivity index and effects of value on BOLD signal in the two L IFG ROIs, but not in the extrastriate ROI.

To test this hypothesis, we converted the activation peaks reported by Kirchhoff and Buckner from Talairach to MNI space (Lancaster et al., 2007), and drew a sphere with an 8 mm radius around each of those peaks. During the cue period, there were no significant main effects of value in any of the 3 ROIs, all ts < 1.76, nor was there a correlation with selectivity index in any of the 3 ROIs, all rs < 0.13. During the word-encoding period, there was a main effect of value in both the anterior L IFG ROI, $t(19) = 5.65$, $p < .001$, and in the posterior L IFG ROI, $t(19) = 3.96$, $p = .001$, but not in the extrastriate ROI, $t(19) = 1.33$. In



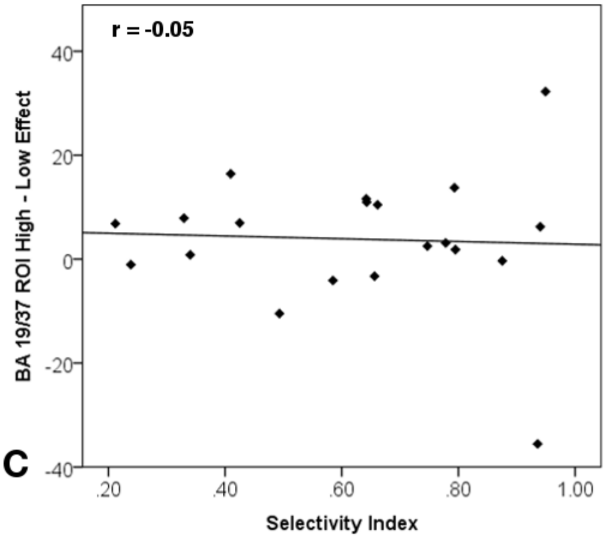


Figure 2.5. Correlations between selectivity index and value effects on BOLD signal in 3 ROIs from Kirchhoff and Buckner (2006): (A) Anterior L IFG (BA 45/47), (B) Posterior L IFG (BA 44/6), (C) Extrastriate visual cortex (BA 19/37). Regions A and B, which have been associated with verbal strategy use, show significant correlations between selectivity index and value effects on BOLD signal. Region C, a visual association area that has been associated with non-verbal encoding strategies (BA 19/37), does not show a significant correlation.

addition, during word encoding, selectivity index correlated significantly with value effects in the anterior L IFG ROI, $r = 0.56$, $p = .010$, and with value effects in the posterior L IFG ROI, $r = 0.61$, $p = .005$, but not with value effects in the extrastriate ROI, $r = -0.05$ (Figure 2.5). Thus, our results are consistent with the idea that participants who exhibit more memory selectivity may be preferentially engaging prefrontally-mediated verbal elaboration strategies during encoding of high vs. low value words.

Individual Differences in Self-Reported Strategies, Selectivity, and Working Memory

To further enhance our understanding of how people tend to strengthen encoding of high-value items, we examined responses to the post-study questionnaires. We first examined and categorized self-reported strategy use at encoding. All participants reported using some type of verbal strategy to try to remember the words. Of these, 14 participants described strategies that would seem to rely on the meaning of the words (e.g., generating stories or images that combined multiple words). The remaining 6 participants described strategies that did not rely on meaning (e.g., rote rehearsal or alphabetizing). Selectivity index did not reliably vary between the groups using these two different strategy types, $t(18) < 1$. Individuals who used meaning-based strategies did recall more high-value words ($M = 9.21$, $SD = 1.57$) than those who used other verbal strategies ($M = 7.48$, $SD = 1.95$), $t(18) = 2.10$, $p = .050$, while not differing on the number of low-value words recalled, $t(18) < 1$. In addition, individuals who used meaning-based strategies tended to have higher working memory (WM) composite span scores ($M = .26$, $SD = .70$) than those who used non-semantic verbal strategies ($M = -.61$, $SD = .85$), $t(18) = 2.40$, p = .027.

Another result that speaks to strategy use is based on whether individuals reported limiting rehearsal exclusively (or nearly so) to high-value items. These reports largely came from people’s descriptions of what they were doing during fixation and vowel-consonant periods. We assume that the distinction between those who exclusively rehearsed high-value words and those who merely preferred rehearsing high-value words during these periods of “down time” reflected similarly divergent strategy use during the word-encoding period. Twelve participants reported largely or entirely ignoring the low-value items, while seven participants reported trying harder on high-value items, but did not appear to ignore low-value items. Finally, one participant reported ignoring value completely. An independent-samples t-test comparing the first two groups (excluding the one person who reported being indifferent to value) showed that selectivity index was significantly higher for individuals who reported that they ignored low-value items ($M = .74$, $SD = .19$) than for those who just tried to focus more on high-value items ($M = .47$, $SD = .22$), $t(17) = 2.80$, $p = .012$. Perhaps unsurprisingly, individuals who reported ignoring low-value items recalled significantly fewer of these items per list ($M = 1.87$, $SD = 1.85$) as compared to those who did not report ignoring low-value items ($M = 4.34$, $SD = 2.96$), $t(17) = 2.25$, $p = .038$. The two groups did not reliably differ on the number of high-value items recalled, however, $t(17) < 1$.

These findings led us to further examine individual differences in high-value vs. low-value recall. We found that selectivity index shows a highly significant negative correlation with low-value recall ($r = -.72$, $p < .001$), while the expected positive correlation between selectivity index and high-value recall does not reach significance ($r = .26$). We compared the absolute values of these r coefficients via a test of dependent correlation coefficients (Stieger, 1980), and found that the correlation between selectivity index and low-value recall is significantly stronger than the correlation with high-value recall, $t(18) = 2.40$, $p = .03$. Thus, our selectivity index measure is more strongly driven by the number of low-value items recalled than the number of high-value items recalled.

We also examined more closely the relationship between selectivity and WM span. We find that WM span score does not significantly correlate with selectivity index ($r = .25$), similar to the null effect shown by Castel et al. (2009). We also see dissociations in how selectivity and WM affect memory as a function of value. We used linear regression analyses to determine the degree to which selectivity and WM jointly predict high-value recall and, separately, low-value recall. We find that WM span is a strong positive predictor for high-value recall (β = .66, p = .002), but selectivity index is not (β = .09, p = .61). In contrast, WM span is a positive predictor of low-value recall (β = .33, p = .048), while selectivity index is a strongly negative predictor (β =-.81, p < .001). Thus, it seems that higher WM span is generally associated with better recall, consistent with prior work (e.g., Rosen & Engle, 1997; Unsworth, Brewer, & Spillers, 2013). At the same time, selectivity seems to be primarily associated with the degree to which people avoid encoding low-value items. These findings suggest that selectivity relies on strategic control processes that are, at least to some extent, separable from working memory.

Discussion

Prior neuroimaging studies have demonstrated the functional contributions of left ventrolateral prefrontal cortex to deep semantic processing and to the use of verbal elaboration strategies during memory encoding. Here, we demonstrate that activity in this region (specifically in left inferior gyrus and ventral portions of the left middle frontal gyrus) is greater during encoding of high-value words. We also demonstrate a correlation between neural effects of value in this region and a behavioral expression of memory selectivity.

An association between effects of value on BOLD signal and memory selectivity is specifically apparent in regions of L IFG for which individual differences in activity have previously been associated with individual differences in the use of verbal encoding strategies (Kirchhoff & Buckner, 2006). Others have additionally shown that L IFG is specifically involved in control processes related to semantic retrieval (e.g., Thompson-

Schill et al., 1997; Badre et al., 2005; see Badre & Wagner, 2007 for review). Our findings thus provide suggestive evidence that people who selectively encode the most valuable items tend to do so by being more selective in the degree to which they engage semantic encoding strategies when encoding items deemed to be more valuable, relative to items that are less valuable. Subjects with high selectivity frequently reported that they tried to ignore low value items, and this was reflected in greater differences in brain activity in these left hemisphere regions during encoding of high vs. low-value words.

The effect of value on activity in posterior portions of the middle temporal gyrus (pMTG) also correlated with individual differences in memory selectivity. There is prior evidence relating this region with controlled retrieval of semantic knowledge as well. For instance, Wagner, Paré-Blagoev, Clark, & Poldrack (2001) found that searching for a weak semantic associate led to increased activity in pMTG, as well as increased activity in both anterior and posterior portions of left IFG, compared to searching for a strong semantic associate. Badre et al. (2005) observed a similar effect of semantic relatedness on both MTG and LIFG, but also found evidence suggesting that MTG activity reflects retrieval of semantic knowledge, but that only activity in LIFG mediates semantic control processes per se. More recent work has supported a somewhat different viewpoint that both regions play a necessary role in control processes related to retrieval of semantic knowledge, rather than pMTG activity only reflecting retrieval of semantic knowledge itself. For instance, Whitney, Kirk, O'Sullivan, Lambon Ralph, & Jeffries (2011) found that virtual lesions temporarily induced by transcranial magnetic stimulation (TMS) in either left IFG or left pMTG led to similar impairments to performance when judging weak semantic associates, but did not impair performance in judging strong semantic associates. The fact that the degree of increased activity during high-value encoding in both LIFG and pMTG is associated with memory selectivity in the present task, then, provides additional evidence that successfully enhancing memory for high-value items in our value-directed remembering task depends on strategic engagement of semantic processing.

An automated meta-analysis using Neurosynth (http://neurosynth.org; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) provides further evidence suggesting that the regions in which activity is modulated by value in the present study are typically involved in semantic processing. Specifically, a "reverse inference" statistical map generated from peak coordinates from the 670 neuroimaging studies in the Neurosynth database that most heavily utilized the term "semantic", and which formally quantifies the probability that the term "semantic" would be associated with activation in these regions (Figure 2.6), looks strikingly similar to the regions associated with encoding of high-value words in the present study (Figure 2.3B). The meta-analytic map also reflects many of the same regions in which the degree of increased activity during encoding of high-value words correlates

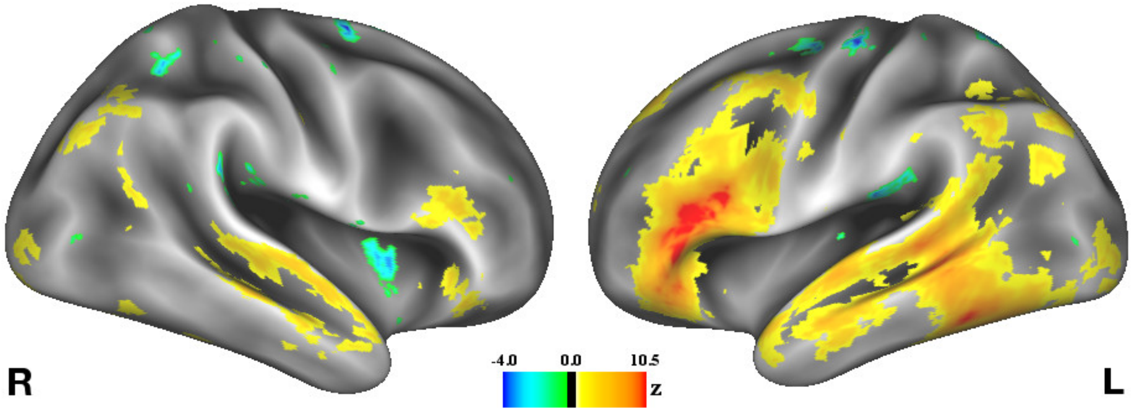


Figure 2.6. Automated Neurosynth meta-analysis of semantic processing. Voxel intensity values reflect the statistical likelihood that any given study reporting an effect in that voxel would be a study that heavily utilized the term "semantic." Note the correspondence between the left PFC and posterior lateral temporal regions that emerged in this meta-analysis and our effects reported in Figures 2.3B & 2.4.

with memory selectivity. Thus, the automated meta-analysis supports the view that memory selectivity arises from differential semantic processing of valuable items.

Selective encoding could potentially be mediated via a selective increase in the use of verbal strategies during encoding of high-value words, or via a selective reduction in verbal strategy use during encoding of low-value words. We observe that selectivity is reliably associated with the degree to which people self-report ignoring low-value words, and that selectivity index is more strongly associated with reduced memory for low-value words than with increased memory for high-value words. Thus, it seems likely that, at least in young adults, selectivity is primarily modulated by the degree to which people disengage semantic processing during encoding of low-value items, rather than by how effectively they encode high-value items.

At the same time, we observe that memory for high-value words and self-reported engagement of semantic encoding strategies is reliably associated with WM span, but these measures are not reliably associated with selectivity. One possible reason for the association between high-value recall and WM capacity is that individuals with high WM span may be better able to implement deep encoding of new high-value items while also simultaneously maintaining previous items. High WM span individuals may also be better able to maintain important items in memory while simultaneously performing the vowel-consonant task that occurred between successive word encoding trials. While these WM mechanisms do seem to be related to higher point totals, they do not seem to be a major factor in selective encoding.

It is also worth noting that we did tend to find greater activity in reward-sensitive regions (specifically, functionally-defined NAcc/ventral striatum and midbrain regions, and an anatomically-defined VTA region) on high-value trials than on low-value trials across participants. The VDR paradigm differs from most studies of reward-motivated learning in that we incentivize high-value items with higher point values, rather than using rewards that have external value (e.g., money). The observation that high point values still lead to increased activity in dopaminergic reward regions, similar to that observed with monetary rewards, supports our assumption that points are sufficiently rewarding to motivate changes in behavior. Indeed, memory performance was very sensitive to point value. This finding is similar to what is observed in a number of real-world contexts (e.g., video games, sports), in which people are motivated by the prospect of a high score. Our findings do, however, differ from past work in that the strength of dopamine-driven reward effects during the anticipatory cue period did not correlate significantly with individual differences in memory selectivity, Rather, in our data, this relationship was only apparent during the phase of the task when participants actually encountered the words. Previous work also suggests that the effects of activity in mesolimbic dopamine regions on subsequent memory are most apparent after a delay (e.g., Spaniol et al., 2014; Murayama and Kuhbander, 2011), perhaps due to their dependence on off-line consolidation mechanisms. Such findings imply that the role of mesolimbic dopamine regions on value-induced memory enhancement should not be apparent in the immediate free recall measure used in the VDR. We believe that our findings of strategic enhancement of encoding and free recall relate to a second mechanism for value-related memory enhancement. This additional mechanism may be complementary to the dopaminergic enhancement of memory consolidation that has been demonstrated by others (e.g., Adcock et al., 2006; Murty et al., 2012; Wolosin et al., 2012), but the two different mechanisms appear to make varying contributions to memory performance based on the time scale and the type of information to-be-remembered.

Finally, our results suggest important potential implications for research on cognitive aging. Castel et al. (2002, 2007, 2009, 2013) found that healthy older adults generally show an excellent ability to be selective in the VDR task. Indeed, older adults often have equivalent memory to young adults for the most valuable items, despite recalling fewer items overall. This pattern of data often yields a higher selectivity index for older adults than that shown by young adults for tests of short-term memory. Thus, whatever older adults do to selectively encode high-value items in the VDR paradigm, they clearly seem to be relying on processes that are not substantially degraded by healthy aging. It may be that older adults retain the ability to be selective in their engagement of the semantic encoding strategies mediated by left PFC, which would provide important evidence about the type of processing that older adults are typically able to engage successfully. Thus, an important direction for future research is to examine age-related differences and similarities in the neural mechanisms of value-directed remembering.

While dopaminergic reward systems play an important role in memory formation, it is also important to consider how the strategic control of frontally-mediated encoding processes serves to selectively enhance memory for valuable items. Particularly in situations in which the delay between study and recall is relatively short, and when the items that need to be memorized are amenable to selective use of verbal encoding strategies, we might expect differential strategy use to be a more important contributor to memory performance than dopaminergic modulation of hippocampal activity. We anticipate that future work will help to determine the specific situations that preferentially engage these respective mechanisms, and whether they independently or interactively contribute to memory performance.

CHAPTER 3

Neural evidence for age-related similarities in semantic processing, but differences in proactive control, during value-directed memory encoding[3]

In Chapter 2, we examined how reward affects verbal memory under conditions that encourage the adoption of different encoding strategies for high-value and low-value items. We found that the degree to which value affects memory on a subsequent free recall test correlates with value-related differences in activity in a largely left-lateralized network of brain regions: L ventrolateral prefrontal cortex (VLPFC)/inferior frontal gyrus (IFG), L posterior lateral temporal cortex, bilateral posterior medial prefrontal cortex/pre-supplementary motor area (pre-SMA), and L caudate. All of these regions have been associated with semantic processes (Binder, Desai, Graves, & Conant, 2009), which we believe are being modulated as part of a conscious strategy to deeply encode the high value words (Galli, 2014). Thus, our results—collected from a sample of healthy young adults—were the first to emphasize that reward can modulate memory via the intentional, differential use of effective encoding strategies, beyond its role in activating the mesolimbic dopamine system.

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[3] This chapter is adapted from a manuscript that has been submitted for publication, currently under review, co-authored with Jesse Rissman, Nanthia Suthana, Alan Castel, and Barbara Knowlton.

We thank Saskia Giebl for assistance with recruiting and running participants, Garth Carlson for publicizing our recruitment materials, as well as Aimee Drolet Rossi and Gregory Samanez-Larkin for suggestions related to task design.

Portions of this work were presented at the 21st annual meeting of the Cognitive Neuroscience Society, Boston, MA, at the 44th annual meeting of the Society for Neuroscience, Washington, DC, and at the Scientific Research Network for Decision Neuroscience and Aging (SRNDNA) conference in Miami, FL.

Effects of Aging on the Relationship between Item Value and Memory Performance

Another important question is how the cognitive and neural mechanisms by which value affects memory encoding change across the lifespan. Prior work has not directly addressed how the neural mechanisms of this process change in older adults. However, there is some relevant behavioral work. For instance, Spaniol et al. (2014) presented older and younger adults with a version of the task paradigm used by Adcock et al. (2006), in which value is believed to affect memory predominantly by increasing activation in the mesolimbic dopamine system. Spaniol and colleagues found no interaction between age and value on hit rates in a subsequent recognition test, meaning that high-reward conditions led to similar improvements in memory across age groups, despite overall poorer memory in older adults, and despite evidence that dopaminergic neurons in the midbrain typically degrade with aging (Bunzeck et al., 2007).

Castel and colleagues (Castel et al., 2002; Castel et al., 2009) have examined how age affects value-based modulation of memory in a context in which subjects must prioritize recall of high value information (see also Hayes et al., 2013). Although older adults do recall fewer items than young adults in these studies, their *selectivity index*, a measure of how strongly value affects memory, tends to be as high, or in some cases even higher, than that seen in young adults. Thus, regardless of the mechanism by which value affects memory, healthy older adults appear to retain the ability to remember the things that are most important to the task at hand even as their overall memory gets worse.

Temporal Shifts in Brain Activity with Aging

One key question that we address in the present study pertains to the timing of value-related activity changes. Namely, are activity modulations triggered immediately in response to the cue stimuli that indicate the value of an upcoming word, or do these modulations occur later, during presentation of the word itself? We are also interested in understanding how these temporal patterns may change with age. Adcock et al. (2006) found increased activity in reward-sensitive regions and in medial temporal lobe (MTL) structures during high-value cues, relative to low-value cues, as well as a subsequent memory effect for high-value items in particular. Although there were value-related differences in MTL activity during stimulus presentation, they did not find value effects in reward regions during presentation of the to-be-remembered picture stimuli. The importance of activity in dopaminergic regions, particularly during the cue period, follows from animal work showing that exposure to dopamine agonists a few minutes prior to stimulus presentation can lower the threshold for long-term potentiation (LTP) in the hippocampus (e.g., Li, Cullen, Anwyl, & Rowan, 2003). Thus, there is a mechanistic explanation for why strengthening of encoding would specifically occur for items presented *after* a reward cue (although see Murayama and Kitagami, 2014, for an example of putative dopamine-driven memory enhancement in humans when the memory stimulus is presented prior to the reward).

Other prior research has shown that brain activity in MTL and neocortical regions in response to a cue indicating how to encode an upcoming item can also differ as a function of subsequent memory status. One such study used electroencephalography (EEG) to measure event-related potentials (ERP) evoked in response to cue stimuli signaling the need for an imminent semantic decision about an upcoming word (Otten, Quayle, Akram, Ditewig, & Rugg, 2006). The magnitude of these pre-stimulus ERP effects in frontal and posterior regions of the cortex was linked to the subsequent mnemonic fate of these items.

Gruber and Otten (2010) examined how pre-stimulus ERP effects are affected by reward, and found a diffusely-localized pattern of more positive ERP activity during high-value cues relative to low-value cues, particularly when the high-value words that followed a given cue were later recognized with high confidence. Pre-stimulus activity was not associated with better memory when the cue was low-value, however, suggesting that these pre-stimulus effects are sensitive to motivation. Other studies have used functional magnetic resonance imaging (fMRI) to examine effects of pre-stimulus activity on subsequent memory, allowing for better localization of where the relevant activity is taking place. Subsequent memory effects in response to pre-stimulus cues have been shown bilaterally in MTL (Park & Rugg, 2010), as well as in lateral prefrontal cortex (PFC) and lateral/medial parietal cortex (Addante et al., 2015). These authors have suggested that subsequent memory effects based on pre-stimulus activity likely result from the adoption of a "preparatory set", in which the brain is more prepared to engage effective encoding operations once the to-be-remembered item appears.

There is reason to believe that older adults might be less able to benefit from pre-stimulus cues than young adults. For instance, Bollinger, Rubens, Zanto, & Gazzaley (2010) showed that young adults tend to show more fusiform face area (FFA) activity, and more connectivity between FFA and fronto-parietal control regions, in response to a cue that the to-be-encoded item about to appear is a face, compared to when no informative cue is presented or when the cue indicates that a scene is about to appear. Memory for face stimuli, in response to an immediate working memory probe and also after a 30-minute delay, was better when such a cue was presented, and the degree of cue-related memory benefit was correlated with the degree of enhanced connectivity between FFA and specific fronto-parietal regions. Thus, the increase in FFA/fronto-parietal connectivity, induced by presentation of the informative cue, appears to have strengthened encoding in young adults. Older adults did not show a change in FFA activity or connectivity in response to the cue, nor did they show memory benefits in response to the cue (Bollinger, Rubens, Masangkay, Kalkstein, & Gazzaley, 2011). Based on these findings, Bollinger et al. (2011) proposed an "expectation deficit hypothesis of cognitive aging," suggesting that an inability to utilize informative cues underlies some aging-related cognitive deficits.

Other work has suggested that older adults tend to rely more heavily on activity later in a trial to compensate for a lack of activity in response to an earlier cue. Dew, Buchler, Dobbins, and Cabeza (2012) found such a pattern in MTL and left dorsolateral PFC (DLPFC) regions during a memory retrieval task. Specifically, young adults show more activity than older adults during a pre-stimulus cue indicating what type of stimulus will need to be retrieved, while older adults show more activity later in the trial, during memory retrieval. Dew et al. refer to this pattern as an Early to Late Shift in Aging, or ELSA.

The results shown by Dew et al. could be considered an extension of the Dual Modes of Control theory (Braver, 2012; Braver, Gray, & Burgess, 2007; Braver, Paxton, Locke, & Barch, 2009), which has been influential in the domain of cognitive control, to the domain of memory retrieval. Braver et al. (2009) found that young adults are more likely to keep a task set in working memory in anticipation of relevant stimuli appearing later, referred to as a proactive mode of cognitive control. By contrast, older adults tend to use a more reactive mode of cognitive control, waiting to engage cognitive control mechanisms until the appearance of a stimulus for which control is required. Based on this prior literature, we might expect that when participants encode to-be-remembered words, as in the present study, young adults will be more likely to show value-related changes in brain activity during the value cues that precede the words, while older adults will only show value-related differences in activity after the word appears.

Spatial Shifts in Brain Activity with Aging

Another important focus of the present study is on how aging might lead to shifts in the localization of value-related differences in encoding-related activity, either in an attempt to compensate for aging-related deficits, or as a consequence of those deficits. Logan, Sanders, Snyder, Morris, and Buckner (2002) found, for instance, that older adults typically show less activity in the left VLPFC than young adults when asked to remember words. However, the difference largely disappears when the depth of semantic processing is controlled by the experimenter. Logan et al. (2002) also found that unlike young adults, for whom VLPFC activity was largely left-lateralized during word encoding, older adults showed nearly as much activity in right VLPFC as in left VLPFC when they did engage this area. Logan et al. concluded that the right hemisphere activation was due to less efficient processing. This interpretation, known as dedifferentiation, implies that an aging-related reduction in lateralization and/or neuroanatomical specialization contributes to deficits in cognitive functioning (see also Li, Lindenberger, & Sikström, 2001).

Cabeza (2002), however, proposed that activity in the contralateral hemisphere is an attempt to compensate for degradation in the areas in which processing is typically performed. There is striking evidence in favor of compensation in certain contexts. For instance, Cabeza, Anderson, Locantore, & McIntosh (2002) used a retrieval task in which the key contrast showed activity in right anterior PFC and right DLPFC in young adults. In lower-functioning older adults, activity was still entirely right-lateralized. High-functioning older adults showed a different pattern, however, recruiting left anterior PFC in addition to right anterior PFC.

During encoding, as opposed to at retrieval, activity tends to be more left-lateralized in young adults, and the evidence has been more mixed as to whether reduced prefrontal laterality in older adults (such as that observed by Logan et al., 2002) reflects compensation. Rosen et al. (2002) found support for the compensation account; they compared semantic encoding blocks to shallow encoding blocks, and found greater enhancement of right VLPFC activity on semantic blocks in higher-performing older adults, relative to young adults and lower-performing older adults. At the same time, others (e.g., Rossi et al., 2004) have found evidence that activity in the contralateral hemisphere is not beneficial for left-hemisphere-dominant encoding tasks, but it does support performance in right-hemisphere-dominant retrieval tasks.

A somewhat different perspective on how aging affects PFC function has been proposed by Rajah and D'Esposito (2005); specifically, they suggest that effects of aging vary by region. In VLPFC, increased bilateral recruitment does not seem to enhance performance (e.g., Logan et al., 2002), and thus those activations likely reflect either dedifferentiation or failed attempts at compensation. However, there does not appear to be a primary functional deficit in this region in older adults; when VLPFC is properly engaged, older adults can perform successfully on tasks relying upon this region. By contrast, in dorsal and anterior PFC, there is a distinction across hemispheres. In the right hemisphere, there seems to be a true functional deficit with aging; even when these regions are activated, they do not contribute to task performance in older adults. In the left hemisphere, by contrast, more dorsal and anterior PFC regions seem to be able to compensate for dysfunction in the homologous right hemisphere regions.

The Present Study

In the present fMRI study, we examine whether brain activation associated with value-related selectivity in healthy older adults differs from that in younger adults in terms of its temporal and spatial pattern. While older and younger adults often exhibit a similar degree of selectivity on the value-directed remembering task, it is unclear if the neural mechanisms supporting selectivity are the same. Because selective remembering of valuable information is relatively preserved in older adults, this paradigm is a particularly appropriate one in which to examine neural mechanisms of compensation in the aged brain.

Method

Participants

Twenty-five older adults were recruited to participate in the study via flyers posted at the UCLA Medical Center, and via flyers and newsletter postings in the broader West Los Angeles and San Fernando Valley communities. Data from two participants were excluded from all analyses due to neurological abnormalities detected during scanning (one cavernoma, one meningioma).

The remaining 23 older adult participants (mean age = 68.70 years, SD = 5.72 years, range = 60-80 years; 13 female) were all right-handed native English speakers with no neurological abnormalities. In addition, none of these individuals reported currently taking psychoactive medication for a major psychiatric disorder. All participants scored at least a 27 on a version of the Mini-Mental State Exam (Folstein et al., 1975), and had either normal or corrected-to-normal vision. Written informed consent was obtained from each participant, and all procedures were approved by UCLA's Medical Institutional Review Board. Participants were paid a base rate of $15/hour, plus additional bonus money based on performance on two additional tasks that were conducted during the same session; these two tasks were performed after the main experiment and are not reported here. For two participants, complete data sets were only available for 4 out 5 functional scanning runs (due to time constraints and technical difficulties, respectively). Finally, behavioral data from the practice session were unavailable for 2 individuals.

Procedures

The task paradigm, scanning procedures, data preprocessing, and the initial fMRI analysis methods were identical to those used in our previous study of young adults, reported in Chapter 2. Thus, only methods that were unique to the analyses reported in this chapter are described here.

To examine age differences in the effects of value throughout the brain, we included young adults and older adults in a single group-level analysis, assigning young and older adults to different regressors, and also labeling them as belonging to separate variance groups. Because we were specifically interested in how aging impacts the expression of value-induced activity modulations, we masked the resulting contrasts to only include voxels that showed value effects in one or both age groups; voxels that failed to show significant effects of value in either age group were excluded. For ROI analyses, we compared young adults with older adults using independent samples *t*-tests on the mean COPE estimates extracted from the high-value vs. low-value comparison. By always conducting across-group contrasts of within-subject COPE values, we avoided direct comparison of BOLD signal levels across age groups, which can be problematic due to differences in vascular reactivity (Samanez-Larkin and D'Esposito, 2008).

To correct for multiple comparisons in our ROI analyses, we applied a Bonferroni-Holm correction (Holm, 1979) across all ROIs for which we performed a particular analysis. All effects survived this correction unless otherwise indicated. Separate analysis types (e.g., main effects vs. correlations, and cue vs. word period) were treated as independent from each other for the purposes of this correction, as were the two age groups.

In order to characterize the temporal evolution of BOLD signal within individual ROIs, we ran a separate GLM analysis, modeling the data using finite impulse response (FIR) basis functions, as a supplement to the more standard GLM analysis described in Chapter 2. For this model, we separated high-value and low-value trials, with each trial beginning at the time of cue onset. We modeled each trial as 10 single time points over a temporal window lasting 25 s from cue onset. Other parameters were the same as for the previously described GLM analysis. This FIR analysis generated separate parameter estimate maps for each 2.5 s peristimulus time bin for each condition, within a given run. For any given ROI, these parameter estimates could be averaged across voxels and runs, and then averaged across participants to yield group-level peristimulus time course plots.

Results

Behavioral Data

We begin by examining how value affected the proportion of items recalled on the free recall tests in older adults (Table 3.1).[4] A 2 x 5 (value x list) repeated measures ANOVA

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[4] Two older adults and one young adult were excluded from the value x list analysis that follows because we only had usable data for 4 out of 5 lists from these individuals, as noted above.

showed a highly reliable main effect of value (high vs. low), *F* (1, 20) = 30.68, *MSE* = .160, $p < .001$, $\eta_p^2 = .61$ (Figure 3.1A). There was also a reliable main effect of list, *F* (4, 80) = 3.64, *MSE* = .013, $p = .009$, $\eta_p^2 = .15$, reflecting generally poorer performance on the first scanned list compared to later lists (Table 3.1). The value x list interaction approached, but did not reach, significance, *F* (4, 80) = 2.08, *MSE* = .012, $p = .091$, $\eta_p^2 = .09$. Planned comparisons confirmed that high-value items were remembered better than low value items across each of the 5 scanned lists, all *ts* > 4.30, $p < .001$. We also used separate paired-samples *t*-tests to examine value effects on the practice lists (Table 3.1). On the first practice list, there was not a reliable main effect of value, *t* (20) = 1.48, $p = .154$, but the effect of value was reliable by the second practice list, *t* (20) = 3.27, $p = .004$.

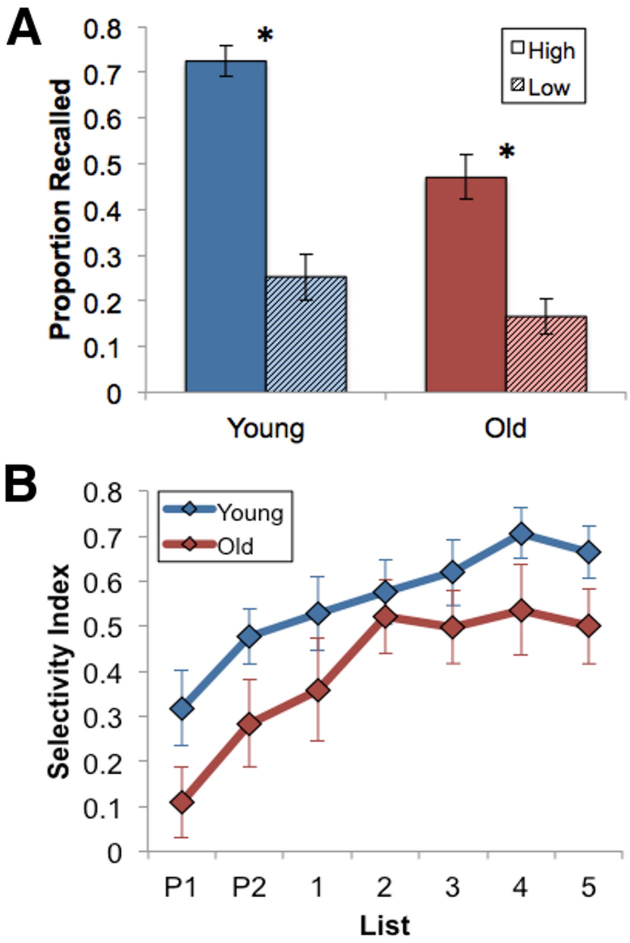

Figure 3.1. (A) Mean proportion of items recalled per list, collapsed across all scanned lists. (B) Mean Selectivity Index as a function of list for young and older adults, including the two initial practice lists (P1 and P2) and the 5 scanned lists. Error bars represent +/- 1 SE.

We also examined whether the proportion of items differed as a function of different point values within high-value and low-value groups in older adults, collapsing across lists (Table 3.2). A one-way repeated measures ANOVA examining only low-value items showed no effect of point value, *F* (2, 44) < 1. On high-value items, there was a trend towards an effect of value, but this effect did not reach significance, *F* (2, 44) = 2.60, *MSE* = .010, *p* = .086, η_p^2 = .11. In addition, the trend that was present was for better memory on 10-point items, not the advantage for 12-point items that might be expected if learners were showing sensitivity to points within the high-value group (Table 3.2). These results justify collapsing across values to form dichotomous high-value and low-value conditions, as we did in Chapter 2 with the young adult data.

Table 3.1. Mean (SE) proportion of items recalled on each list (including 2 practice lists), split by age group and value group.

		List						
		P1	P2	1	2	3	4	5
Young	High	0.500 (0.056)	0.675 (0.048)	0.646 (0.059)	0.693 (0.039)	0.713 (0.045)	0.804 (0.035)	0.763 (0.044)
	Low	0.242 (0.031)	0.283 (0.039)	0.275 (0.055)	0.241 (0.054)	0.242 (0.047)	0.254 (0.060)	0.263 (0.062)
Old	High	0.306 (0.051)	0.484 (0.050)	0.363 (0.054)	0.487 (0.052)	0.492 (0.051)	0.421 (0.057)	0.461 (0.060)
	Low	0.234 (0.041)	0.258 (0.052)	0.129 (0.029)	0.154 (0.035)	0.146 (0.041)	0.150 (0.045)	0.118 (0.025)

Table 3.2. Mean (and SE) proportion of items recalled across the five scanned lists by specific point value.

	Low Value			High Value		
	1	2	3	10	11	12
Young	0.248 (0.047)	0.258 (0.051)	0.253 (0.051)	0.701 (0.039)	0.708 (0.035)	0.764 (0.031)
Old	0.135 (0.026)	0.152 (0.035)	0.133 (0.036)	0.463 (0.055)	0.411 (0.052)	0.458 (0.050)

As mentioned above, *selectivity index* provides another useful metric to quantify the impact of item value on memory recall performance. One-sample t-tests showed that selectivity index was significantly greater than zero across each of the 5 scanned lists in our sample of older adults (all *t*s > 3.14, all *p*s < .005), and a one-way repeated measures ANOVA showed that selectivity index did not reliably change across these 5 lists, *F* (4, 76) = 1.06, *MSE* = .071, $p = .38$, $\eta_p^2 = .05$ (Figure 3.1B). We also examined selectivity index on the two practice lists separately. On the first practice list, selectivity index was not reliably greater than zero, $t(18) = 1.38$, $p = .184$, but on the second list it was greater than zero, $t(20) = 2.95$, $p = .008$.[5]

Finally, we compare memory performance for young and older adults, collapsing items across lists. A 2 x 2 (value x age) mixed ANOVA with repeated measures on the first factor, on the proportion of items recalled, showed a value x age interaction, *F* (1, 41) = 5.34, *MSE* = .028, $p = .026$, $\eta_p^2 = .12$, such that the effect of value on memory was weaker for older adults than for young adults (Figure 3.1A). There was also a main effect of age on memory, *F* (1, 41) = 11.65, *MSE* = .054, $p = .001$, $\eta_p^2 = .22$, with older adults remembering fewer items than young adults (Figure 3.1A). When comparing the weighted average selectivity index across age groups in a separate analysis, there was an apparent trend for older adults to have a somewhat lower selectivity index (Figure 3.1B). However, this difference was not statistically significant, $t(41) = 1.70$, $p = .096$. While we cannot rule out the possibility that there is some aging-related decline in selectivity index in this version of the task, a null effect would replicate prior work (e.g., Castel et al., 2009). More importantly, the fact that older adults showed a reliably positive selectivity index while performing the task in the scanner suggests that they were able to use value effectively in this version of the task.

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[5] Note that selectivity index cannot be computed for a given list if zero items were recalled on that list, as was the case for the first practice list in two participants, and on at least one scanned list for two participants, which is why df varies for corresponding analyses.

Whole Brain fMRI Analyses

Word-encoding period. First, we examined main effects of value across the entire brain in older adults during the word-encoding period (Figure 3.2A; Appendix B—Table B.1A). This analysis revealed a number of areas with greater activity during encoding of high-value words than during encoding of low-value words, including ventral and posterior portions of the left PFC and areas of left lateral temporal, left parietal, and bilateral occipital cortex. In addition, one cluster within the angular gyrus was less active during encoding of high-value words (Figure 3.2A; Appendix B—Table B.1A), presumably reflecting default-mode network deactivation (e.g., Raichle et al., 2001).

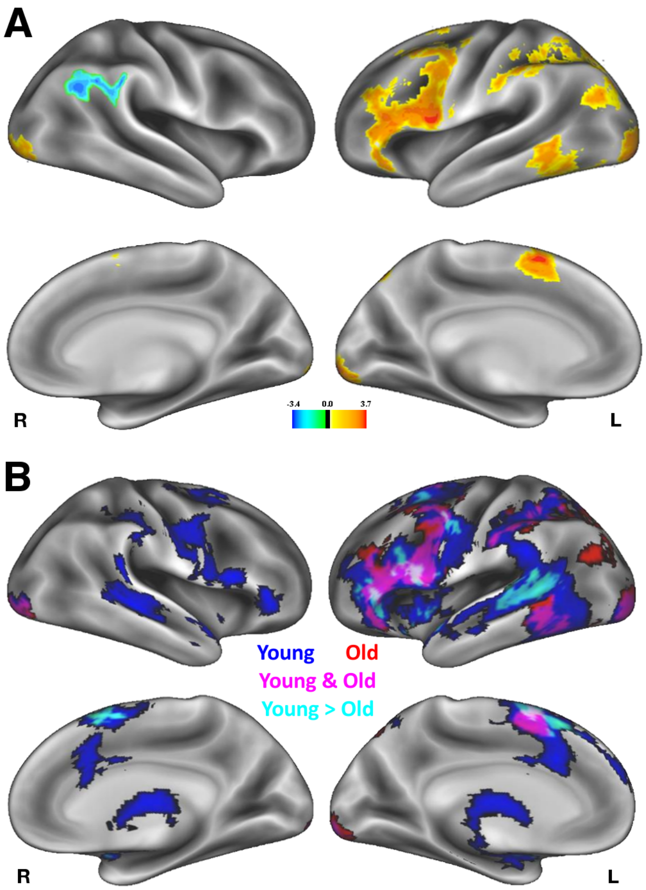

Figure 3.2. (A) Areas in which activity differs for high-value words relative to low-value words during the word-encoding period in older adults. (B) Comparison across age groups of positive effects of value during the word-encoding period, showing effects in young adults (blue) and in older adults (red). Areas of overlap across age groups are in magenta. Areas active in young adults for which effects are significantly stronger in young adults than in older adults are in cyan. Areas in which cyan and magenta colors overlap are in white.

When comparing these effects to the analogous contrast in young adults, we find considerable overlap across the two age groups, including in the ventral and posterior regions of left lateral PFC (Figure 3.2B; Appendix B—Table B.2A). However, despite these commonalities, there were some notable differences. One theoretically important difference is that, while young adults show reliable effects of value in right lateral PFC, older adults do not. Theories of reduced hemispheric asymmetry in older adults (e.g., Cabeza, 2002) would make the opposite prediction. That is, Cabeza's HAROLD model would predict that older adults should show a more bilateral pattern of activity than young adults, but in fact, older adults seem to show an even stronger left-lateralization than do young adults in this task. Thus, our data do not support the idea that older adults compensate for neural deficits by engaging the hemisphere contralateral to the one in which a task is typically performed.

Other age-related differences are also apparent. Specifically, the spatial extent of value-related activity modulations is generally less diffuse in older adults. For example, young adults show value effects in caudate nucleus that are not found in older adults. Additionally, we find statistically reliable age differences in the degree to which activity in left IFG, left superior temporal gyrus, and bilateral pre-supplementary motor area (pre-SMA) are modulated by value. Even in some portions of left IFG that show value effects in both age groups, there are regions in which those effects are reliably stronger for young adults. Finally, one cluster near the parietal/occipital junction (precuneus/cuneus) shows greater deactivation on high-value items relative to low-value items in young adults relative to older adults (Appendix B—Table B.2B); this region is likely part of the default-mode network (cf., Persson et al., 2007).

Exploring main effects of value is a start for understanding how encoding-related activity is modulated by value. However, this analysis does not tell us which value-related differences in activity at encoding actually lead to more selective memory for valuable items. One way to address that important question is to correlate value-related differences in brain activity with selectivity index across individuals. That is, we are looking for regions in which greater value-related differences in brain activity at encoding are associated with stronger behavioral effects of value on subsequent memory. As mentioned above, we previously reported a correlation between selectivity index and value-related modulation of activity in a largely left-lateralized network of prefrontal and temporal regions in young adults (Figure 2.4). The next question, then, is whether older adults show a similar pattern of results.

We indeed find that in older adults, there is a left-lateralized network of regions for which value-related differences in activity correlate with selectivity index (Figure 3.3A; Appendix B—Table B.3). Specifically, we find clusters consistent with this pattern in L ventral and posterior lateral PFC, L posterior lateral temporal cortex, and L pre-SMA. Thus, there is evidence

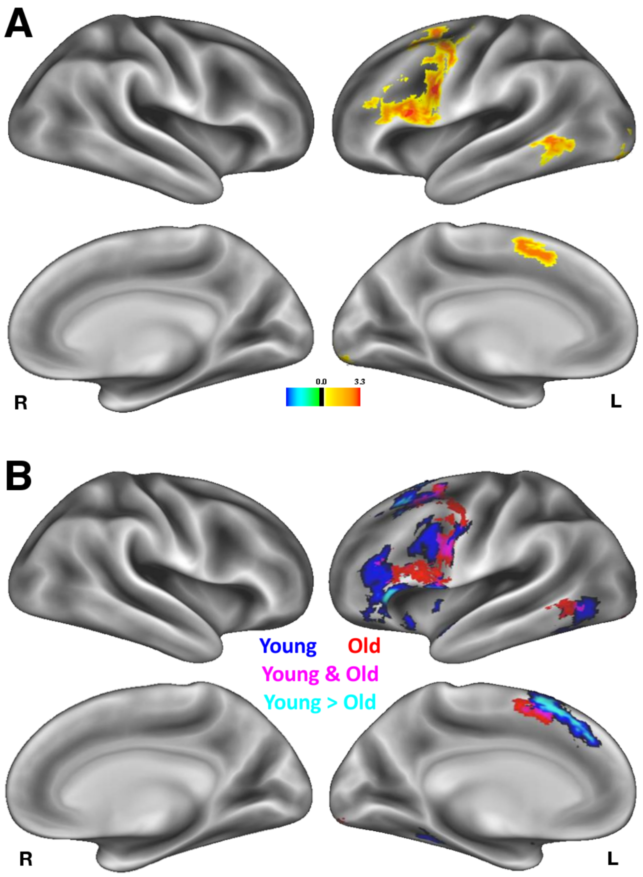

Figure 3.3. (A) Areas showing a brain-behavior correlation between effects of value during the word-encoding period and selectivity index in older adults. (B) Comparison across age groups of brain-behavior correlation effects during the word-encoding period. As in Figure 2, young adult effects are in blue and older adult effects are in red. Areas of overlap across age groups are in magenta, while areas active in young adults for which effects are significantly stronger in young adults than in older adults are in cyan.

that value-related modulation of semantic processing is associated with the degree of memory selectivity in both age groups.

When we compare these results directly with the analogous brain-behavior correlation analysis in young adults (Figure 3.3B; Appendix B—Table B.4), however, we do see some subtle but potentially important differences. One area in which the correlation with selectivity is significantly stronger in young adults than in older adults is in the most anterior portion of pre-SMA (colored in cyan in Figure 3.3B). At the same time, more posteriorly in the SMA, there is an effect in older adults that is not reliably present in young adults, although here there is no reliable age difference. A cluster in the most ventral portion of the left IFG also shows a significant interaction with age, with young adults but not older adults showing a reliable correlation between selectivity index and the degree of value-related activity modulation. Additionally, the left prefrontal regions that showed the maximal correlation effects appear to be shifted in a dorsal and posterior direction in older adults as compared to young adults, although there is not a statistically significant age difference other than in the small ventral IFG cluster noted above.

Cue period. In young adults, we previously identified a number of regions exhibiting increased activity during the cue period of the trial when the cue signaled that the upcoming item would have high value, versus low value, if later remembered (Chapter 2; Figure 2.3A). These cue-period value effects—observed in high-level control areas such as left lateral PFC and reward-sensitive regions such as nucleus accumbens—overlapped somewhat with the network of regions showing main effects of value during the word-encoding period. Interestingly, a whole brain analysis conducted on our present sample of older adults revealed no main effects of value during the cue period; i.e., no regions showed significantly greater or lesser activity in response to high value cues. When directly comparing activity between young adults and older adults for this contrast, there were prefrontal, parietal, and occipital clusters that emerged as showing a reliable value x age interaction, such that the effects of value were larger in young adults than in older adults (Figure 3.4; Appendix B—Table B.5). Thus, it seems clear that older adults are much less responsive to value during the cue period than are young adults. These age differences may reflect broader age differences in the deployment of anticipatory cognitive control processes.

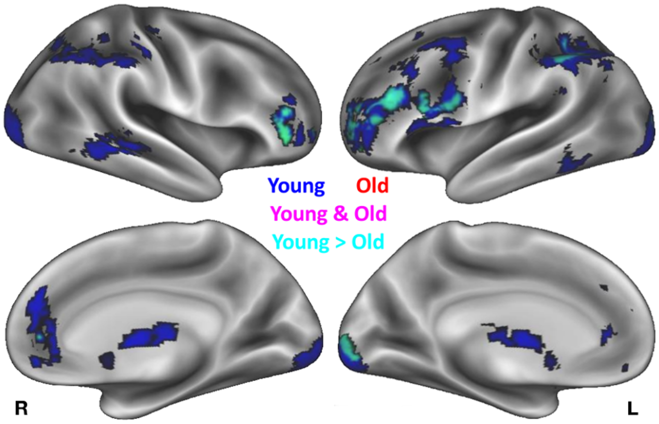

Figure 3.4. Main effects of value during the cue period. Regions showing value effects in young adults are in blue; of these areas, regions in which value effects are significantly greater in young adults than in older adults are in cyan. No areas showed value effects during the cue period in older adults.

We next ran a whole-brain analysis searching for any brain regions in which value-related differences in activity during the cue period were associated with individual differences in selectivity index. In neither the young nor the older adult groups did we find any reliable clusters showing correlations between value-related activity differences and memory selectivity during the value cue period, before the to-be-remembered word was presented. Thus, our findings differ from earlier studies that emphasized how, in young adults, a stronger brain response to a pre-stimulus cue is associated with better subsequent memory for the item that appears immediately after that cue (e.g., Adcock et al., 2006, Park and Rugg, 2010, Bollinger et al., 2010; Addante et al., 2015). Instead, in our paradigm, value-related differences in the brain response to the cue appear to be inconsequential for later memory in both age groups. Based on prior literature, it seems likely that pre-stimulus preparatory activity, and any age-related differences in the deployment of these mechanisms, are more consequential in other tasks than they are in the present paradigm (cf., Bollinger et al., 2011).

Region of Interest Analyses

In order to better understand the patterns of effects seen in the whole brain analyses, we also performed ROI analyses to investigate the engagement of networks supporting semantic processing and reward during performance on this task. Our ROI analysis involved clusters of regions gathered from automated meta-analyses using the Neurosynth database (http://neurosynth.org; Yarkoni et al., 2011). We generated “reverse inference” maps from the database for the terms “semantic” and “reward”. We chose to examine the “semantic” network based on our hypothesis that preferential engagement of deep semantic processing is one important strategic mechanism for bolstering the memorability of high value words. This allowed us to define an ROI for further analyses that is not statistically dependent on our whole-brain results. We also generated a “reward” network ROI, in order to facilitate comparisons with prior relevant studies that focused on such a mechanism (e.g., Adcock et al., 2006). Note that in both cases, we use the term “ROI” not to refer to a single focal region of interest but rather to a larger mask that encompasses several different brain areas.

The initial maps generated by the Neurosynth software included voxels that were more likely to be activated in the studies with a given index term than would be expected by chance, with an FDR-corrected threshold of $p < .01$. Out of 9721 total studies in the database, 701 were indexed with the term “semantic” and 497 were indexed with the term “reward”. To ensure that the resulting ROIs were not excessively diffuse in their spatial extent, we applied an additional voxelwise threshold of z > 5.20, producing an alpha level of p < .0000001, one-tailed. The “semantic” ROI included 4501 voxels, and produced a network that included large areas of L inferior frontal gyrus and L lateral temporal cortex (Figure 3.5). The “reward” ROI included 3827 voxels, and produced a network including bilateral nucleus accumbens, ventral tegmental area, and ventromedial PFC (Figure 3.9A).

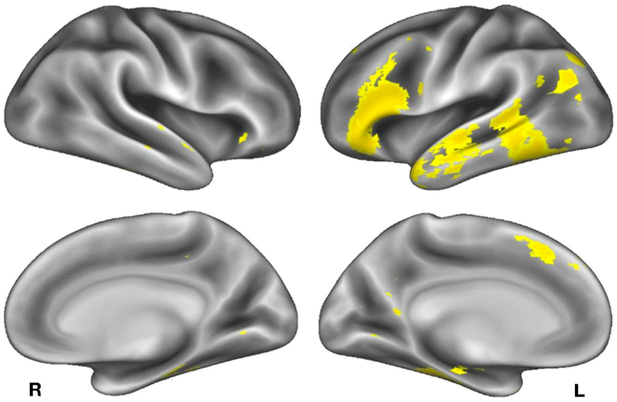

Figure 3.5. Map of Neurosynth-derived semantic network ROI.

Neurosynth Semantic ROI. We first examined how activity across the Neurosynth-derived semantic network ROI is associated with main effects of value, and how these value effects correlate with selectivity index. During the word-encoding period, activity within the semantic network ROI was reliably greater for high-value items, both in young adults, $t(19) = 4.94$, $p < .001$, and in older adults, $t(22) = 3.55$, $p = .002$ (Figure 3.6A). The value x age interaction approached significance, $t(41) = 2.01$, $p = .051$, suggesting that the effect may be somewhat stronger in young adults. We also examined how value-induced modulation of activity in this semantic network ROI relates to selectivity index. The magnitude of value-related changes in brain activity in the semantic ROI during the word-encoding period correlated with selectivity index in young adults, $r = .54$, $p = .015$ (Figure 3.6C), as well as in older adults, $r = .57$, $p = .005$ (Figure 3.6E). These findings suggest that in both age groups, the magnitude of value-related differences in the degree to which a given individual activates semantic processing areas of the brain during word encoding correlates with how selective they are as a function of value at the time of the recall test.

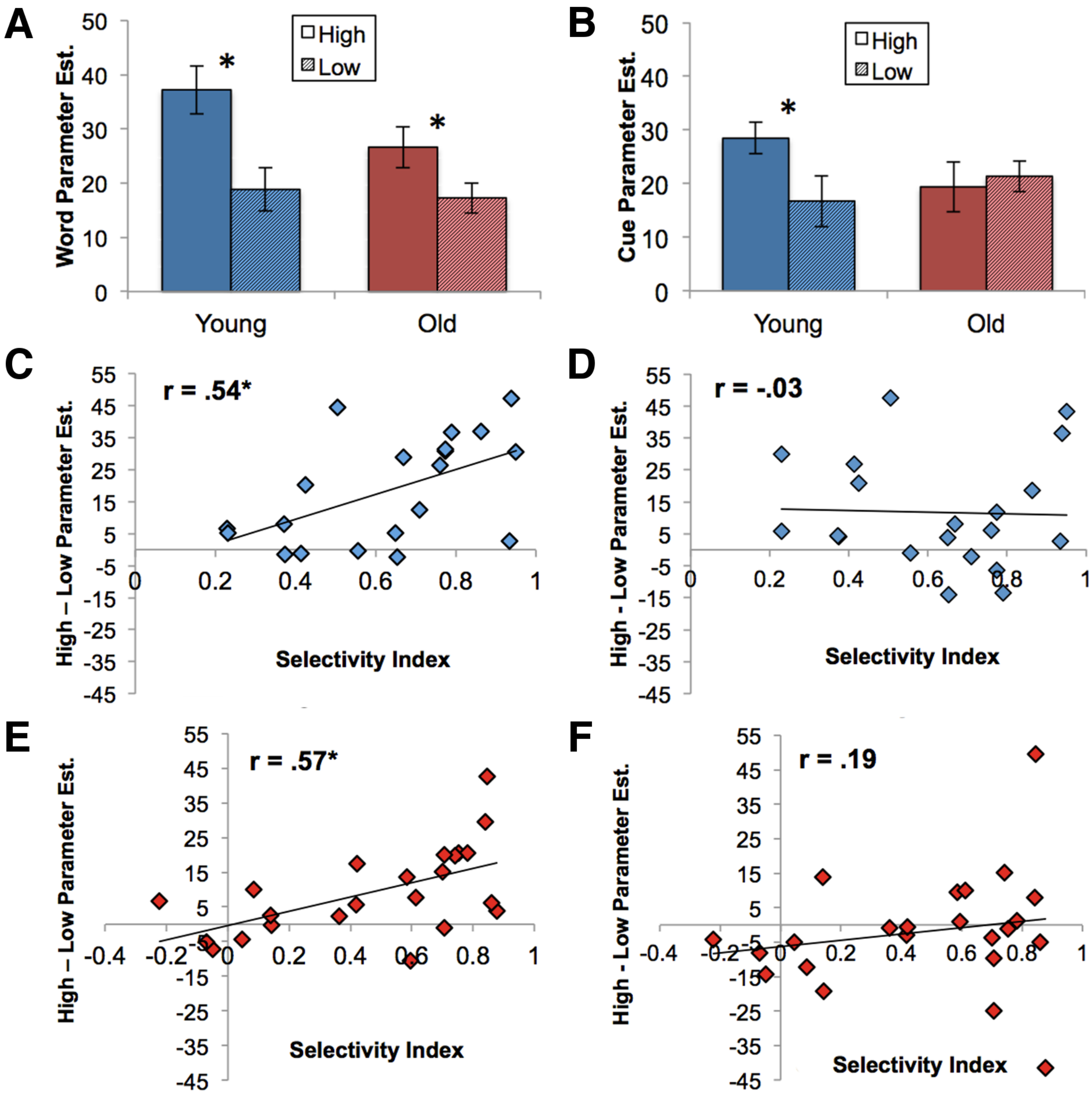

Figure 3.6. (A, B) Activation parameter estimates for each value condition and age group, averaged across the Neurosynth semantic ROI, during (A) word period and (B) cue period. Error bars represent +/- 1 SE. (C-F) Correlations between effect of value on activation parameter estimates and selectivity index. (C) Young adults, word period; (D) Young adults, cue period; (E) older adults, word period; (F) older adults, cue period.

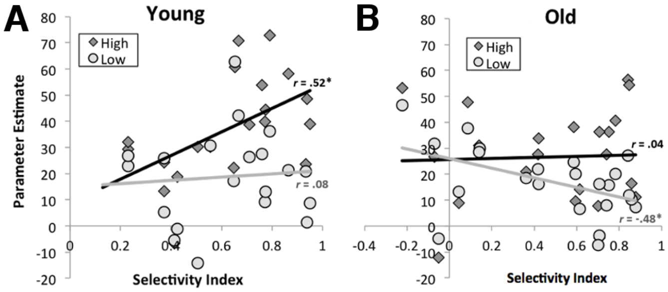

Figure 3.7. Correlations between selectivity index and brain activity within the Neurosynth semantic-processing ROI during the word encoding period for high-value and low-value items, in (A) young adults and (B) older adults.

We do, however, see interesting age-related differences when examining how encoding activity for high and low value words, relative to baseline, is differentially related to subsequent selectivity. In young adults, activity during encoding of high-value words correlated positively with selectivity, *r* = .52, *p* = .018, while activity during encoding of low-value words was uncorrelated with selectivity, *r* = .08, *p* = .736 (Figure 3.7A). We compared the two correlation coefficients via a test of dependent correlation coefficients (Steiger, 1980), and found that the difference was significant, *t*(18) = 2.60, *p* = .018. In older adults, activity during encoding of high-value words was uncorrelated with selectivity index, *r* = .04, *p* = .860, but activity during encoding of low-value words was significantly negatively correlated with selectivity index, *r* = -.48, *p* = .019 (Figure 3.7B). The difference between the correlations is significant, *t*(21) = 4.69, *p* < .001. Thus, it seems that in young adults, selective recall is associated with stronger activation of semantic-processing regions, relative to baseline, during encoding of high-value words, while in older adults, selective recall is associated with reduced activation of semantic processing regions, relative to baseline, during encoding of low-value words.

Another important age difference emerged during the cue period. Young adults showed greater activity for high-value cues, *t*(19) = 2.97, *p* = .008, while older adults showed no effect of value on cue period activity, *t*(22) = -0.56, *p* = .585 (Figure 3.6B). We also found a reliable value x age interaction during the cue period, *t*(41) = 2.58, *p* = .013, confirming that young adults show a significantly stronger effect of value than older adults. Cue period activity did not correlate with selectivity index in young adults, $r = -.03$, $p = .888$ (Figure 3.6D), nor did cue period activity correlate with selectivity index in older adults, $r = .19$, $p = .392$ (Figure 3.6F). Thus, there were striking age differences in how value affected brain activity during the cue period, consistent with differences in proactive control in response to the value cue. Still, despite the fact that value-related differences in activity across this same network during the word-encoding period strongly correlated with memory selectivity, value-related differences in activation during the cue period did not appear to contribute to this selectivity.

In addition to the standard GLM analysis, we used a finite impulse response (FIR) model to generate peristimulus time course plots of BOLD signal averaged across the semantic network ROI. This analysis makes no a priori assumptions about the shape and timing of the BOLD signal associated with component stages of the task. Thus, it allows for a stronger test of our contention that the apparent age differences in how value affected brain activity during different stages of the trial (cue period vs. word period) reflect a true difference in older adults' cognitive responses, rather than, for example, a generally slowed HRF in older adults. Visual inspection of Figure 3.8A finds a value-related difference in activity early in the trial, 2.5-7.5 seconds after cue onset, in young adults, which likely corresponds to the brain response to the cue. Older adults do not appear to show a differential response during that same time period (Figure 3.8B). Later in the trial, however, 10-12.5 seconds after cue onset, it is apparent that both young adults and older adults show a notably stronger BOLD signal during high-value trials, compared to low-value trials. We can assume that this change in BOLD signal is in response to the

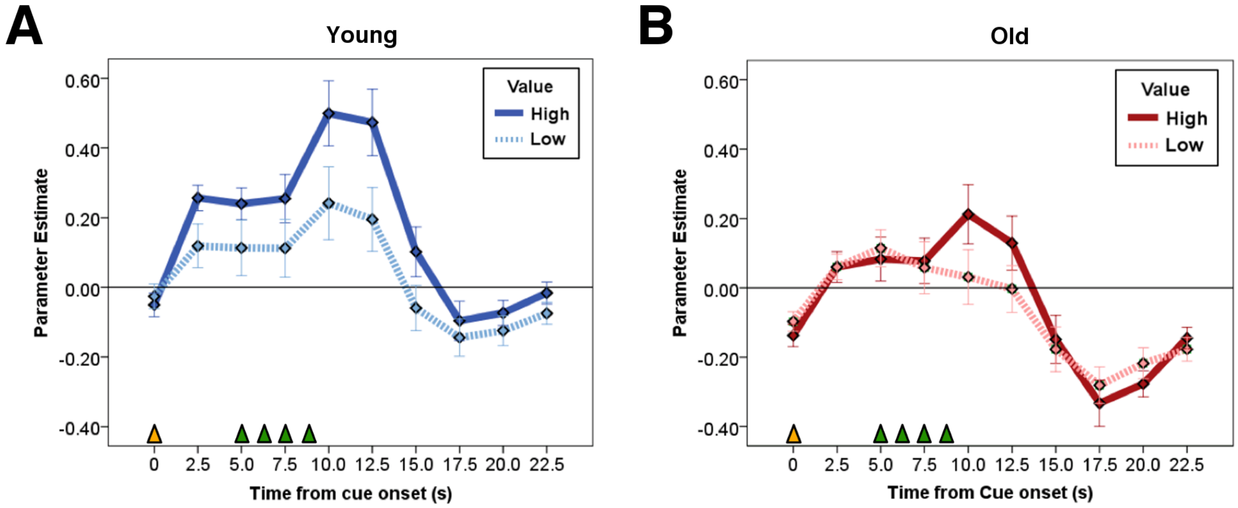

Figure 3.8. Peristimulus plots generated using an FIR model, for (A) young adults and (B) older adults, showing brain activity in the Neurosynth-derived semantic processing ROI. Error bars represent +/- 1 SE. Cue onset occurs at time 0, as indicated by an orange triangle; activity 2.5-7.5 s after cue onset is likely driven primarily by the brain response to the cue. Word onset was jittered, and was equally likely to occur 5, 6.25, 7.5, or 8.75 s after cue onset, as indicated by green triangles on the X axis. Activity 10-12.5 s after cue onset is likely to reflect brain response to the word.

appearance of the word on the screen, which occurs between 5 and 8.75 seconds after cue onset. From 15 s to 22.5 s after cue onset, the last part of the modeled time window, both brain activity and the value-related difference in activity is greatly reduced in both age groups. It appears that by this point in the trial, encoding-related activity for the newly-presented item is largely complete, with no age-related slowing of the BOLD response visible in older adults.

Paired-samples t-tests on the mean parameter estimates at each time point, with a Bonferroni-Holm correction for multiple comparisons applied for the 10 time points within each age group, confirm the above description of the results. There was no value-related difference in activity at the first time point (0 s) for either age group: $t(19) < 1$ in young adults, and $t(22) = 1.36$, $p = .19$ in older adults. In young adults, there was a significant value-related difference in activity at the next three time points: time point 2 (2.5 s), $t(19) =$

2.88, $p = .010$, time point 3 (5 s), $t(19) = 2.97$, $p = .008$, and time point 4 (7.5 s): $t(19) = 2.89$, $p = .009$. In older adults, there were no value-related differences in activity at any of these three time points, all ts < 1. A 2 x 2 (value x age) mixed ANOVA, with repeated measures on the first factor, examining the parameter estimates averaged across these three time points, confirms that there is a value x age interaction, $F(1, 41) = 7.09$, $MSE = .015$, $p = .011$. Thus, the FIR analysis replicates the results from our standard model-based GLM analysis (Figure 3.6B), indicating that young adults show effects of value during the cue period while older adults do not.

We next interrogated FIR activity estimates obtained from time points 5 (10 s) and 6 (12.5 s), which presumably reflect the brain response to the appearance of the to-be-remembered word stimuli, based on the large increase in activity relative to baseline. Young adults show a significant effect of value on BOLD signal during time point 5, $t(19) = 5.07$, $p < .001$, and time point 6, $t(19) = 4.12$, $p = .001$. Older adults also show a significant effect of value on BOLD signal during time point 5 (10 s), $t(22) = 3.52$, $p = .002$, and time point 6 (12.5 s), $t(22) = 2.94$, $p = .008$. A 2 x 2 (value x age) mixed ANOVA on the average parameter estimates across these two time points shows that the value x age interaction is not significant, $F(1, 41) = 2.55$, $MSE = .026$, $p = .118$. Thus, both young adults and older adults show more activity during high-value items than during low-value items when responding to the to-be-encoded word, again replicating the results from our GLM analysis (Figure 3.6A).

Finally, we examine how value affected brain activity towards the end of each trial, 15-22.5 s after cue onset. This period is critical to rule out the alternate explanation that the HRF response to value is generally slowed in older adults. During time point 7 (15 s), young adults showed a significant value effect, $t(19) = 2.70$, $p = .014$, while older adults did not, $t(22) < 1$. Value effects during the final three time points (17.5 s, 20 s, and 22.5 s) were not significant for either age group, all $|t|$s < 1.77. A 2 x 2 (value x age) mixed ANOVA on the parameter estimates averaged across the final four time points found a marginally significant value x age interaction, $F(1, 41) = 3.87$, $p = .056$. However, the trend, if anything, is for stronger value effects in young adults, contrary to the idea of a general slowing of the hemodynamic response in older adults. Therefore, this potential alternate explanation for the observed age-related difference in the temporal extent of responsiveness to value is unlikely to explain our findings. Instead, it seems clear that the effect of value is more temporally limited in older adults than in young adults, supporting our conclusion that older adults only show differential brain activity as a function of value while the word is on-screen, and not in response to the cue.

Neurosynth Reward ROI. We also examined how value affects activity in reward-sensitive regions, specifically using the Neurosynth-derived reward ROI (Figure 3.9A). During the word-encoding period, we found that young adults show a main effect of value, $t(19) = 4.14$, $p = .001$, while older adults do not, $t(22) = 1.45$, $p = .16$ (Figure 3.9B). There is a trend for a value x age interaction during the word period, $t(41) = 2.10$, $p = .042$, but this effect does not surpass the multiple-comparison-corrected α of .025. Additionally, young adults showed a correlation between selectivity index and effect of value in the reward ROI during the word period, $r = .54$, $p = .013$, while older adults did not, $r = .21$, $p = .344$.

Young adults also showed a main effect of value during the cue period, $t(19) = 3.15$, $p = .005$, while older adults did not, $t(22) < 1$; here, the value x age interaction was significant, $t(41) = 2.63$, $p = .012$ (Figure 3.9C). However, in the cue period, there was no correlation

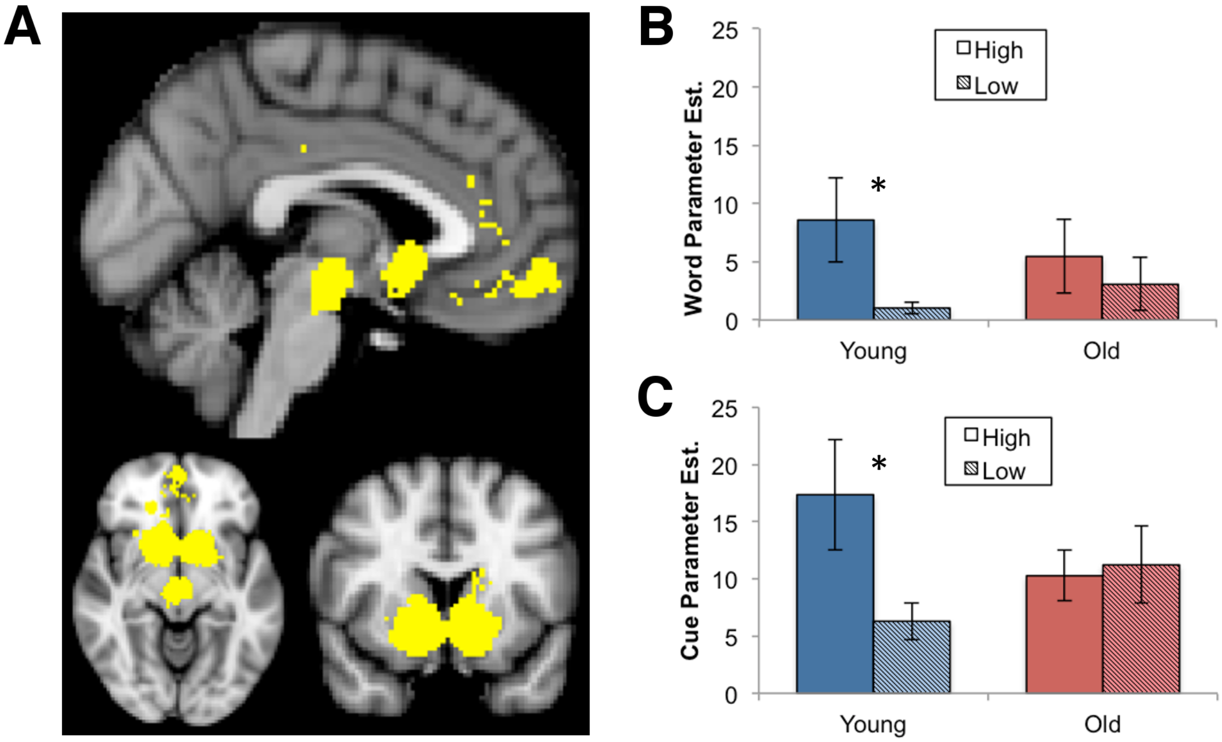

Figure 3.9. (A) Map of Neurosynth-derived reward network ROI. (B, C) Parameter estimates for each value condition and age group, averaged across the Neurosynth reward ROI, during (B) word period and (C) cue period. Error bars represent +/- 1 SE.

between selectivity index and the effect of value in the reward network ROI in young adults, *r* = -.09, nor in older adults, *r* = .11. Young adults therefore reliably show greater activity in reward-sensitive regions during both high-value words and during the cues that precede high-value words, relative to low-value words. These value-related differences in activity seem to affect selectivity in later recall when they happen during word encoding, but not when they precede encoding. Older adults do not show any sensitivity to value in reward-sensitive regions, suggesting that their performance on this task may be less driven by anticipation of potential future rewards than is the case for young adults.

Supplemental Region of Interest analyses

Left Hemisphere Prefrontal. Because the Neurosynth-derived network ROIs include a heterogenous mix of structures, we also replicate some of our critical ROI analyses using more localized, spherical ROIs. To more carefully examine semantic-processing areas in the prefrontal cortex, we use two prefrontal ROIs that we also used in Chapter 2: one in ventral/anterior L inferior PFC (BA 45/47), and the other in dorsal/posterior L inferior PFC (BA 44/6), both spheres with radius 8 mm. The central voxel of each ROI was derived from an earlier meta-analysis of encoding-related activity (Konishi, Donaldson, & Buckner, 2001; see also Buckner & Logan, 2002), and activity in both ROIs has previously been associated with the use of verbal strategies during encoding (Kirchhoff & Buckner, 2006; see also Logan et al., 2002), making them particularly relevant to our questions of interest.

In L BA 44/6, we found a main effect of value during the word-encoding period in both age groups: young adults, $t(19) = 3.96$, $p < .001$, and older adults, $t(22) = 3.28$, $p = .003$, with no age x value interaction, $t(41) = 1.36$, $p = .18$. We also found a correlation between effects of value on brain activity and selectivity index in both age groups: young adults, $r = .61$, $p = .005$, and older adults $r = .65$, $p = .001$. In the L BA 45/47 ROI, we again found a main effect of value during the word-encoding period in both age groups: young adults, $t(19) = 5.65$, $p < .001$, and older adults, $t(22) = 2.92$, $p = .007$. This effect tended to be stronger in young adults than in older adults, $t(41) = 2.42$, $p = .020$. Young adults also showed a significant correlation between value effects and selectivity index, $r = .55$, $p = .012$, while this effect did not reach significance in older adults, $r = .40$, $p = .061$. However, a Fisher r to z transformation shows that the difference between correlation coefficients for the two age groups was not significant, $z < 1$.

Thus, word period effects in the spherical prefrontal ROIs were largely similar to what we saw in the Neurosynth-derived ROI. The most notable aging-related finding to emerge from this set of analyses is that the main effect of value and the correlation with selectivity both tended to be somewhat weaker for older adults than for young adults, though not significantly so, in the more anterior prefrontal ROI, while being more similar across age groups in the dorsal/posterior prefrontal ROI. This finding provides some additional support for the conclusion that emerged from our whole-brain data, that older adults performing a selective memory encoding task seem to rely less on anterior/ventral portions of lateral PFC than do young adults, while relying as much or more strongly on posterior/dorsal portions of lateral PFC.

During the cue period, main effects of value were not significant in either prefrontal ROI in young adults: in BA 44/6, $t(19) = 1.76$, $p = .095$, nor in BA 45/47, $t(19) = 1.48$, $p = .156$. There also was not a main effect of value during the cue period in either ROI in older adults, $|t|$s < 1. In addition, there were no correlations with selectivity index in either ROI for either age group, rs ≤ 0.28. Thus, the key cue-period age differences found in the larger semantic ROI do not appear to replicate in the more focal left prefrontal ROIs.

Right Hemisphere Prefrontal. Using localized prefrontal ROIs also allows us to test hypotheses about contralateral compensation (e.g., Cabeza, 2002), as we can test the cross-hemisphere mirror image homologues of our left prefrontal ROIs. Our approach follows that used by Logan et al. (2002), in which the L and R hemisphere BA 44/6 ROIs with the same peaks as our ROIs showed reduced laterality in older adults. Here, we wanted to determine whether older adults have a stronger tendency than young adults to selectively activate right-hemisphere prefrontal regions when encoding high-value items, and whether any value-related differences correlate with selectivity index.

In the R BA 44/6 ROI, neither age group shows a main effect of value during the word encoding period, $t < 1$ in both age groups. In the R BA 45/47 ROI, we do find a main effect of value in young adults during word encoding, $t(19) = 4.79$, $p < .001$, but this effect is not found in older adults, t(22) < 1, and the value x age interaction is significant, $t(41) = 2.98$, $p = .005$. Thus, young adults show value-related modulation of activity during encoding in the R anterior prefrontal ROI, while older adults do not, the opposite of what would be predicted according to a contralateral compensation account. There was also no correlation between selectivity index and value-related modulation of activity for either ROI in either age group, all $|r| < .19$, indicating that any value-related differences in R hemisphere prefrontal activity that are present do not seem to contribute to enhanced memory selectivity at recall.

We found no reliable main effects of value in either of the two right prefrontal ROIs in either age group during the cue period, all $|t| < 1.73$, nor were there correlations between selectivity index and value-related differences in activity in either ROI for either age group, all $|r| < .22$. In combination with the whole-brain data, there is, therefore, a distinct lack of evidence to suggest that older adults show a more bilateral pattern of value-related changes in prefrontal activity relative to young adults during encoding in this task. Indeed, if anything, it seems that young adults show more of an increase in activity in right prefrontal regions during high-value trials than do older adults.

Supplemental Reward ROI—Nacc. The reward-sensitive ROI as we defined it in Neurosynth also includes a somewhat heterogenous mix of structures, including some voxels in prefrontal cortex, which may not all reflect pure reward responsiveness. To address this issue, we also ran ROI analyses using a bilateral NAcc ROI defined from the

Harvard-Oxford probabilistic structural atlas. For this ROI, we included any voxels that were more likely to be a part of the NAcc than of any other subcortical structure. With this ROI, we found similar effects as with the larger, Neurosynth-based reward ROI, but also see some subtle differences. Specifically, we found that during the word-encoding period, activity was greater for high-value items than for low-value items in young adults, $t(19) = 2.40$, $p = .027$, while there was no effect of value in this ROI in older adults, $t(22) = 1.01$, $p = .32$, but there was also no value x age interaction, $t(41) < 1$. Additionally, unlike in the Neurosynth-defined reward ROI, we did not find a significant correlation between selectivity index and value-related differences in activity in young adults, $r = .35$, $p = .126$, nor did we find a correlation in older adults, $r = .23$, $p = .296$. During the cue period, young adults again showed reliably greater activity on high-value items, $t(19) = 4.62$, $p < .001$, while older adults did not, $t(22) < 1$. Here again, we did find a reliable value x age interaction during the cue period, $t(41) = 3.28$, $p = .002$. We also again found no correlation between selectivity index and value-related differences in activity during the cue period in either age group, $|r| < .23$.

Thus, like in the Neurosynth ROI, young adults show main effects of value in NAcc during both the cue period and the word period that are not found in older adults. However, the degree of value-related difference in activity during the cue period again does not correlate with selectivity on the subsequent free recall test in either age group. In addition, while the Neurosynth ROI results suggested that reward-related activity during the word-encoding period in young adults may relate to subsequent memory selectivity, the lack of significance for that effect in the NAcc ROI tempers this conclusion. Still, the stronger finding from this set of analyses is that a value-related difference in activity in reward-sensitive regions is present in young adults but not in older adults.

Discussion

When faced with a daunting number of words to memorize, only some of which are deemed to be highly valuable, both younger and older adults can effectively calibrate their encoding strategy to prioritize these important items. Our fMRI results showcase how individuals of both age groups achieve this selectivity by regulating activity across a common set of left-lateralized brain regions based on the value of the words. These brain areas, which include VLPFC, posterior dorsal medial PFC/pre-supplementary motor area (pre-SMA), and posterior lateral temporal cortex, have all been associated with deep semantic processing (Binder et al., 2009; Binder and Desai, 2011). Specifically, value-related differences in activity in these brain regions during the word-encoding period correlate with selectivity index on the later recall test. We also observe a similar pattern of effects across a semantic processing network ROI derived from the Neurosynth meta-analysis database. Although it is impossible to directly infer psychological processes from brain activity, this profile of results putatively suggests that, similar to young adults (Chapter 2; Cohen et al., 2014), older adults are strategically controlling the degree to which they engage semantic processing during encoding of high-value items relative to the degree of such engagement during encoding of low-value items. Thus, the relative preservation of memory selectivity across the lifespan is accompanied by a general preservation in control of this semantic processing circuit.

It is notable, however, that higher selectivity indices in young adults seem to be driven largely by the degree of *increased* activity in semantic processing regions during encoding of *high-value* words, while selectivity in older adults seems to be tied more closely to what happens during encoding of *low-value* words. Specifically, unlike young adults, older adults seem to show little inter-individual variability in semantic processing activity during encoding of high-value words. Instead, selectivity indices in older adults seem to be higher based how much an individual *refrains* from activating regions related to semantic processing during encoding of low-value words. Thus, there does appear to be an age-related difference in how, precisely, value-related modulation of brain activity in semantic processing regions affects later recall.

Effects during Word Encoding

One important piece of the semantic processing circuit that is differentially engaged depending on stimulus value is in left VLPFC, also described as left IFG. In a number of prior studies (e.g., Wagner et al., 1998; Savage et al., 2001; Paller and Wagner, 2002; Addis and McAndrews, 2006; Kirchhoff and Buckner, 2006; Miotto et al., 2006), activation of left inferior prefrontal regions during encoding in young adults has been associated with the use of effective semantic strategies, as well as with a concomitant increase in performance on a subsequent memory test. More recent work (Kirchhoff et al., 2012; Miotto et al., 2014) has shown that older adults who are trained to engage semantic encoding strategies also show increased activity in left IFG, among other regions, during encoding. It is notable that when we compare the six activation peaks in left IFG from across those two studies (transformed from Talairach to MNI space as necessary; Lancaster et al., 2007) with our whole-brain analysis examining the correlation between value effects during encoding and selectivity index in older adults (see Figure 3.3A), we find that four of the six peaks from these prior studies overlap with significant clusters in our data, and the other two peaks are only one voxel away. Thus, although the critical left IFG effects in the mapwise brain-behavior correlation analysis do not overlap precisely across age groups, there is still solid evidence to suggest that left IFG effects in older adults reflect strategic engagement of semantic processing, similar to what we found previously for young adults (Cohen et al., 2014).

Value-related activity differences in two other areas also show correlations with selectivity index in older adults: posterior lateral temporal cortex, including middle temporal gyrus (MTG), and pre-SMA. Prior work (e.g., Whitney et al., 2011; Wagner et al., 2001) has suggested that processing in both left IFG and left posterior MTG is required for tasks that involve retrieval of semantic information, particularly when the semantic associations are weak, and thus more difficult. The strong influence of pre-SMA in both age groups is also notable. Prior studies have shown that this area is specifically involved in relatively unconstrained, internally-directed semantic generation tasks. For instance, Crosson et al. (2001) found that activity in pre-SMA was more broadly apparent with self-paced covert generation of category members and less apparent when generation was experimenter-paced. Activity was further reduced when cues guided the specific exemplars that were to be produced. Similarly, Tremblay and Gracco (2006) found greater activation in pre-SMA as well as L IFG when participants were asked to generate a word from a broader relative to a narrower category space. Thus, all three of the regions in which value-related modulation of activity during word encoding correlates with selectivity in older adults are relevant to the use of self-generated semantic strategies.

Gazzaley and colleagues have found that older adults have trouble inhibiting processing of irrelevant stimuli, and that the degree to which individual older adults are able to suppress neural responses to irrelevant stimuli correlates with better short-term memory for the to-be-attended stimuli (Gazzaley, Cooney, Rissman, & D'Esposito, 2005; see also Gazzaley, Clapp, McEvoy, Knight, & D'Esposito, 2008; Chadick, Zanto & Gazzaley, 2014). Thus, it may at first blush seem surprising that in the present study, older adults are generally able to modulate encoding-related activity as a function of value and avoid "wasting" encoding resources on low-value stimuli. However, there are important differences between our paradigm and that used by Gazzaley et al. (2005). Most notably, participants in our task must generate retrieval cues for the to-be-remembered items in order to increase the probability that they will later be able to successfully free recall these items. It seems likely that this involves some sort of active process, such as linking semantic features of a given word with other to-be-remembered words. Participants can thus avoid being distracted by less relevant stimuli in a passive manner, by refraining from engaging semantic processing for a given word. This mechanism would seem to be very different from that evoked by the Gazzaley et al. studies, in which participants had to engage in active, top-down suppression of high-level visual processing for face or scene stimuli to avoid being distracted by attention-grabbing irrelevant stimuli.

Age-Related Shifts in Word-Encoding Period Activity

Despite general similarities in the pattern of behavioral and neuroimaging effects shown by older and younger adults in our data, we do also find some clear differences. One reliable age difference is that, when examining areas in which value effects correlate with selectivity index, this association is reliably weaker in older adults in the most anterior portion of the pre-SMA cluster and the most ventral portion of the lateral PFC cluster. Instead, brain-behavior correlation effects seem to emerge more posteriorly in both of these areas in older adults (Figure 3.3B). Notably, prior studies have found strong white matter connectivity between pre-SMA and lateral inferior PFC, particularly in the left hemisphere (e.g., Ford, McGregor, Case, Crosson, & White, 2010). This connection was recently defined as a distinct tract, called the frontal aslant tract (Catani et al., 2012). There is evidence that this tract is important in language production, as damage to it has been correlated with reductions in verbal fluency in aphasia patients (Catani et al., 2013). Other work has shown a rostrocaudal gradient of resting-state functional connectivity between pre-SMA and lateral PFC, such that posterior portions of pre-SMA are more strongly connected with posterior portions of lateral PFC, while anterior pre-SMA is connected with anterior portions of lateral PFC (Taren, Venkatraman, & Huettel, 2011). There is also reason to believe that more posterior connections between these regions are more preserved with aging, as Ford et al. reported that anatomical connections measured by diffusion tractography between left posterior IFG and posterior medial PFC were stronger, relative to more anterior connections between these regions, in older adults than in young adults. Thus, the apparent anterior to posterior shift that we observe in pre-SMA may be part of an overall posterior shift in prefrontal activity in older adults.

The shifts in relevant prefrontal activity seem largely consistent with Rajah and D'Esposito (2005), at least in the general sense that the specific brain regions that are most effective for performing a task may be shifted in older adults due to the uneven rate at which age-related degradation occurs in different prefrontal regions. Another potential aging-related shift in activity that has been described in previous studies is a reduction in hemispheric asymmetry in older adults (e.g., Cabeza, 2002). That pattern would suggest that while value-related differences in encoding-related activity in left hemisphere regions contribute to successful encoding in young adults, older adults might engage right hemisphere regions as well. We failed to find any evidence for such a reduction in laterality. In fact, young adults show a reliable tendency towards increased engagement of right prefrontal regions during encoding of high-value items, while older adults do not (Figure 3.2B). Indeed, the R hemisphere BA 45/47 ROI shows such an effect even more strongly, including a reliable value x age interaction, with a main effect of value showing up in young adults but not in older adults. Thus, our data suggest that older adults are showing, if anything, even stronger laterality than young adults in terms of how value affects encoding-related activity.

Pre-Stimulus (Cue Period) Effects

A striking difference between younger and older adults emerged during the value cue period, before the to-be-remembered word was presented. This difference is partially consistent with both the expectation deficit hypothesis proposed by Bollinger et al. (2011), and with the Dual Modes of Control framework (Braver et al., 2007; Braver, 2012). Bollinger et al. showed that older adults fail to show both the neural response and the behavioral benefit shown by young adults in response to a pre-stimulus cue that can help direct encoding. Braver et al. (2009; see also Paxton, Barch, Racine, & Braver, 2008) showed that older adults tend to respond more reactively, while young adults respond more proactively, in a cognitive control task. Dew et al. (2012) subsequently showed that in a memory retrieval task, older adults tend to be less responsive than young adults to a cue that might lead to proactive retrieval-related processing, and instead show stronger, reactive activity in response to the stimulus itself, consistent with the Dual Modes of Control theory. The degree to which aging affects the timing of neural responses within a trial—during a pre-stimulus cue vs. during the stimulus—has not previously been examined in the context of memory encoding, however.

We find that both during the time period when the value cue is on-screen, and during the immediately following period when the word is on-screen, young adults show stronger engagement in regions related to semantic processing when the cue indicates a high point value. Older adults do not show these effects during the cue period, but they do show greater engagement of these critical semantic processing regions during the word-encoding period for high-value items. Thus, young adults are engaging PFC-mediated control mechanisms on high-value items both proactively and reactively. Older adults, on the other hand, seem to only respond reactively, waiting until they see the word that they need to encode before engaging in differential processing for high-value items.

At the same time, it is important to remember that the degree to which young adults selectively engage left prefrontal regions on high-value items during the cue period does not seem to be associated with selectivity at recall. Thus, in this case, proactive encoding processes do not seem to be beneficial for young adults. This finding is in contrast to prior studies (Otten et al., 2006; Park and Rugg, 2010; Bollinger et al., 2010; Gruber and Otten, 2010; Addante et al., 2015) that have shown that items in which encoding-related processes are engaged proactively are more likely to be remembered on a later test. Thus, we might predict that in other memory paradigms, age differences in the tendency to proactively engage encoding-related activity in response to an informative pre-stimulus cue would contribute to aging-related differences in memory, as was found by Bollinger et al. (2011). Our results additionally suggest that increased proactive control in younger adults does not simply arise in situations where it can effectively enhance performance, but is also present when it is unrelated to task outcomes.

Another notable age difference between young and older adults is in how reward-related regions are activated during encoding. Young adults show strong differences in activity as a function of value both prior to and during encoding (cue period and word period), which are apparent in both the whole-brain analysis and when examining the network of reward-related regions defined as an ROI using the Neurosynth database. In contrast, for older adults, activity within these regions was not modulated by item value during either the cue or the word period. Interestingly, although the magnitude of value-related activity in the reward network ROI during the word period correlated with memory selectivity in young adults, differences in value-related modulation of activity in these same regions during the cue period were not at all associated with the degree to which value affected memory selectivity on the recall test in either age group.

This finding is contrary to prior neuroimaging studies (e.g., Adcock et al., 2006; Gruber et al., 2014a), in which value-related differences in memory were associated with greater activity in reward-sensitive regions prior to the appearance of the to-be-remembered item. However, two major features of our study design may account for the differing results between those studies and the present study. One is that our primary dependent measure was the degree to which people selectively recall high-value items on a free recall test, while prior studies have measured effects of value on recognition memory. In the procedure used here, subjects were required to recall items from successive lists, and became aware of the limited capacity of their recall ability and the need to be selective in order to maximize recall of valuable words. In this context, strategic efforts to modulate the degree to which semantic processing is engaged on high-value vs. low-value items may be a more effective way to enhance the relative memorability of high-value items than is anticipatory activation of a dopamine-hippocampal circuit.

A second difference between our study and other studies of value effects on memory is that we used a very short delay between study and test, with the recall test typically beginning less than 1 minute after encoding was completed for a given list. Adcock et al. (2006) tested memory after 24 hours, and behavioral studies (e.g., Murayama and Kuhbander, 2011; Spaniol et al., 2014) have demonstrated putatively dopamine-driven effects of value on memory performance that are present after a long delay of at least 24 hours, but are not reliably present on a test given at a short delay, up to 10 minutes after study. Other neuroimaging studies (Wolosin et al., 2012; Gruber et al., 2014a) have found dopamine-driven effects of value on memory after a shorter delay, within a single experimental session. Still, even in those experiments, the average delay between study and test was longer than in our paradigm, with an average delay on the order of 20 minutes in both studies. Thus, it is possible that a longer delay would strengthen the degree to which effects of value on anticipatory activity in the dopamine system would relate to how strongly value affects subsequent memory. Additionally, given older adults' general insensitivity to value in dopaminergic brain regions in this study, it is possible that young adults would show a greater selectivity advantage over older adults with a long delay, compared to what we observe here.

It is not clear whether the lack of value-related differences in the proactive engagement of brain regions related to semantic control and reward processing is due to a strategic choice by older adults, which would suggest greater efficiency in older adults than in young adults, or whether it is due to older adults having a reduced ability to spontaneously engage encoding processes proactively. Either way, it seems that young adults may not be proactively recruiting encoding processes in a controlled way to enhance performance, but instead engage in such processes whether or not they are effective. It may be that in young adults, the engagement of proactive control processes is automatic, and not in response to task demands.

However, prior work (e.g., Braver et al., 2009; Bollinger et al., 2011; Dew et al., 2012) has also shown that older adults tend to not respond proactively to stimuli even when such responding is helpful. Thus, it seems likely that older adults' relatively preserved ability to control memory encoding in the value-directed remembering paradigm is related to the ineffectiveness of proactive modulation of encoding-related mechanisms in this paradigm. We can then assume that older adults would likely show a greater decrement in performance than what we observe here if proactive responding to the coming stimulus were effective in achieving the task goals.

Relatedly, it is notable that the primary effective mechanism in achieving memory selectivity, value-modulated engagement of a left-lateralized fronto-temporal network associated with semantic encoding, is essentially preserved across age groups. This preservation across age groups of the most effective mechanism for controlling encoding as a function of value is likely another key piece of the puzzle as to why older adults are able to achieve comparable levels of memory selectivity to young adults. That is, in addition to not employing the mechanisms that appear to be ineffective in young adults, namely, proactive engagement of semantic and reward processing regions, older adults are able to successfully implement the strategy that is effective across both age groups, reactive engagement of semantic processing. Thus, it may be that to optimize the efficiency of memory performance in older adults, they should be given the opportunity to selectively and reactively engage semantic encoding processes for important information.

CHAPTER 4

Neural and cognitive mechanisms made apparent by testing value-directed remembering in a dual process memory context[6]

One theoretical distinction that has shown a great deal of explanatory power in the memory literature is the dissociation between recollection and familiarity. Specifically, some studied items can produce a detailed, episodic recollection, including memory for details of the encoding experience, while other items produce only an enhanced feeling of familiarity relative to unstudied items. Although some disagree, proponents of dual process models of memory have found a great deal of evidence to suggest that recollection and familiarity have different neural substrates, and that they are also differentially affected by manipulations of encoding and retrieval conditions (Yonelinas, 2002; Yonelinas, Ally, Wang, & Koen, 2010). Thus, in order to more fully understand how people encode high-value items differently from low-value items, it is worth examining how value differentially affects recollection and familiarity at the time of a later test.

Empirically Defining and Measuring Dual Processes

Recollection and familiarity can be defined empirically in a number of different ways. The different methods often converge on similar results, but they also each make different assumptions, and thus, when using only one method, it is not possible to know with certainty that a given finding reflects true effects of a manipulation on the underlying recollection and familiarity processes, rather than an artifact from the measurement

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procedure (Yonelinas, 2002). For this reason, it is often advisable to test any particular manipulation across multiple methods.

One of the oldest and most widely-used procedures for dissociating recollection and familiarity is the Remember/Know ("R/K") procedure, first introduced by Tulving (1985). In this procedure, participants are asked at the time of retrieval to distinguish whether they "Remember" seeing a given item, or whether they merely "Know" that they saw that item. Typically, careful instructions are provided, emphasizing that a Remember response should be accompanied by an ability to consciously recollect details of the encoding experience, via episodic memory. A Know response, in contrast, is typically defined as a confident feeling that the item was learned, but without the sense of episodic recollection that accompanies a Remember judgment. It should be noted that both Remember and Know judgments can be high confidence, but the difference is in the episodic quality of the memories.

Dual process theorists, beginning with Yonelinas and Jacoby (1995), have noted a potential problem with the Remember/Know methodology, however. That is, modern dual process theories often assert that the two processes are independent, and may both contribute to memory for a particular item. In the R/K procedure, however, Remembering and Knowing are mutually exclusive; thus, if the participant labels an item as Remembered, there is no way to assess whether there was also a feeling of familiarity associated with that item. To address this issue, Yonelinas and Jacoby proposed a correction to the R/K procedure, in which the proportion of items given an R response is taken into account when estimating familiarity. Typically, a correction for false alarms is applied at the same time, yielding the following formula for corrected familiarity, $F = \frac{K_{hit}}{1-R_{hit}} - \frac{K_{FA}}{1-R_{FA}}$, while recollection is estimated via the formula $R = R_{hit} - R_{FA}$. The assumption being made by the

Yonelinas and Jacoby correction, following from an assumption that the two processes are independent, is that items given an R response are equally likely to show above-chance familiarity as items not given an R response. This contrasts with the assumption inherent in using the raw response proportions, that items given an R response cannot at the same time be remembered on the basis of familiarity.

Although an assumption of complete independence between Remember and Know judgments is arguably inconsistent with intuitive notions about memory, in that a state of recollection *without* familiarity seems difficult to imagine, Yonelinas and Jacoby (1995) provide evidence that the R/K paradigm yields more coherent results in the context of an independence assumption than with an exclusivity assumption (see also Jacoby, Yonelinas, & Jennings, 1997). Specifically, they find that the effects of size congruency on raw Know responses are inconsistent with other measures of estimating familiarity, and that these effects are in fact inconsistent and lacking theoretical coherence. When applying the correction described above, Yonelinas and Jacoby found results that do align well with other methods, as well as leading to more coherent theoretical interpretations. At the same time, others (e.g., Gardiner, Java, & Richardson-Klavehn, 1996) have disagreed strongly with the conclusion that the processes underlying R and K responses should be treated as independent. Subsequently, Knowlton (1998) reported that R items convert to K items after a week-long retention interval more often than the pure versions of either independence or exclusivity would predict. Her findings instead suggested that familiarity is present for both R and K responses, with episodic recollection occurring in addition to familiarity to yield R responses.

Still, more recent work has continued to support the use of this correction when estimating familiarity. Brown and Bodner (2011) found that when participants were asked to independently rate recollection and/or familiarity, deep levels of processing led to an increase on both measures. This contrasted with the results from a standard binary R/K paradigm, in which they found positive effects of a deep level of processing on R responses but negative effects on K responses. When the Yonelinas and Jacoby correction is applied to the data from the standard R/K paradigm, Brown and Bodner see effects on both processes, providing further evidence that the exclusivity assumption inherent to the traditional R/K procedure leads to biased estimates of familiarity.

Additonally, Sheridan and Reingold (2011, 2012) developed a modified R/K paradigm in which participants were presented with a pair of words on a recognition test; on some trials, one word was old while the other was new, while on other trials, both words were new. Participants first had to judge whether one of the words evoked an R or K judgment, and then they had to choose which item was more likely to be old. Encoding was varied based on either generation or levels of processing; both of these manipulations affect the richness of the encoding process. Sheridan and Reingold found that, consistent with prior literature (e.g., Gardiner, 1988), the rate of R judgments was higher for the deeper encoding condition, but the rate of K judgments was not affected by encoding conditions—or, if anything, showed a higher rate of K judgments for the shallower encoding condition. However, forced-choice performance on items given a K response was better for items in the deep encoding condition. This dissociation suggests that the raw rate of K responses is not a valid measure of familiarity-based memory strength in the presence of strong recollection effects. In contrast, when the Yonelinas and Jacoby (1995) correction is applied to the R/K responses, an effect of encoding depth in the expected direction is apparent on familiarity estimates, consistent with data from the forced-choice test. Thus, while either way of scoring responses in the R/K paradigm makes assumptions that may not be fully supported, it seems likely that a corrected estimate of familiarity following Yonelinas and Jacoby provides a better estimate of the underlying familiarity process than does the raw proportion of K responses.

Another way of isolating effects of recollection from familiarity is to examine memory for peripheral details from the encoding event (i.e., source memory), which requires recollection, as compared to item memory that lacks source details, which is assumed to reflect familiarity (Johnson, Hashtroudi, & Lindsay, 1993; Yonelinas, 2002). An advantage of this approach is that it relies on an objective measure of retrieval of encoding context, rather than a subjective report that could be erroneous. However, one disadvantage is that this approach is likely to underestimate recollection and overestimate familiarity, as a person could recollect an item and some details of the encoding context, but not remember the specific contextual details that the experimenter has chosen to test. In addition, it is difficult to isolate estimates of familiarity with this procedure, since item memory can draw upon both recollection and familiarity.

One classic means of using source recollection to separately estimate recollection and familiarity is the process dissociation procedure. In this paradigm, first introduced by Jacoby (1991; Jacoby, Toth, & Yonelinas, 1993), participants study items in two different source contexts, such as in separate lists. Then, two different tests are given, one in which items are to be recalled regardless of source, and another in which items from only a single source are to be recalled. The first test reflects combined effects of recollection and familiarity, while on the second test, recollected items from the list that is not to be recalled will be suppressed, while items for which no source information is available will, in at least some cases, be misattributed to the list that is being recalled. Independent estimates of recollection and familiarity can be derived from performance on the two tests using formulas described by Jacoby et al. (1993).

While the process dissociation procedure provides a clever and powerful way to dissociate recollection from familiarity, it still has limitations. One such limitation is that it relies on a strong assumption of independence between the two processes, which, as noted above, is potentially questionable. An alternative means of dissociating between recollection and familiarity is to test some items using a test that can only be solved via recollection, such as a test of source memory, while testing other items using a test that can only be solved using familiarity. This approach is referred to by Yonelinas (2002) as a task-dissociation method. While familiarity is more difficult to isolate than recollection in this way, one useful property of familiarity for this purpose is that recognition via familiarity tends to occur reliably faster than recognition via recollection (e.g., Hintzman & Curran, 1994; Hintzman & Caulton, 1997; Yonelinas & Jacoby, 1994). The task dissociation approach also makes assumptions, in that the tests must be chosen carefully to ensure that performance is unlikely to be "contaminated" by the process not being tested. However, the approach does have the virtue of being free of any assumptions related to the independence or non-independence of recollection and familiarity.

One more way of dissociating recollection from familiarity is via the use of receiver operating characteristic (ROC) curves. One distinctive aspect of the ROC method is that its estimates of recollection and familiarity are based on a simple recognition test that includes an assessment of memory confidence. An ROC plot can be produced based on the ratio of hits (on the Y axis) to false alarms (on the X axis) at each level of confidence, and a curve can be fit to these points via an algorithm (Yonelinas, 1994). The dual-process signal detection (DPSD) model (Yonelinas, 1994; Yonelinas et al., 2010) that underlies this application of ROC analysis assumes that recollection is a threshold process, which either produces highly confident memories or provides no information at all. Thus, the Y intercept of the ROC curve (i.e., the point at which the false alarm rate is zero) produces an estimate of recollection. In contrast, familiarity strength is assumed to vary for both old and new items, and a signal detection process must be used to set a threshold and determine judgments for individual items. The accuracy of this familiarity process can be determined by estimating *d'* from the degree of curvature in the ROC plot. The qualitative shape of an ROC plot is also considered to be informative, as the degree to which the fitted line curves away from the diagonal indicates greater familiarity, while recognition based on recollection tends to have a higher Y intercept, which leads to increased asymmetry in ROC curves.

Neural Basis of Recollection and Familiarity

An important aspect of dual-process models of memory that has generally, though not universally, been confirmed across various methodologies is that recollection and familiarity are dissociable in the brain (Yonelinas, 2002; Yonelinas et al., 2010). Specifically, recollection is believed to depend on the hippocampus, while familiarity signals are thought to emerge from nearby but distinct regions of the medial temporal lobe (MTL); specifically, the perirhinal cortex (Aggleton & Brown, 1999; Brown & Aggleton, 2001). Some of the strongest evidence for this point comes from a double dissociation observed in brain lesion patients. Yonelinas et al. (2002) showed that patients with hypoxic brain damage, believed to affect only the hippocampus, showed reduced recollection but no reduction in familiarity. In addition, recollection but not familiarity scores were negatively correlated with the severity of the precipitating event. By contrast, patients with brain damage that included both hippocampus and the surrounding MTL cortex showed deficits in both recollection and familiarity. Additionally, the dissociation between recollection and familiarity was apparent across multiple methods: Remember/Know, ROC, and dissociating free recall from recognition. Similar findings have been replicated in other studies (e.g., Mayes, Holdstock, Isaac, Hunkin, & Roberts, 2002; Turriziani, Fadda, Caltagirone, & Carlesimo, 2004; Aggleton et al., 2005). Although the theoretically complementary neuropsychological profile, a lesion that affects perirhinal cortex but not hippocampus, is rare, Bowles et al. (2007) tested such a patient using a remember-know test, ROC analysis, and speeded recognition. Across all 3 methods, this patient showed the pattern that would be predicted by the DPSD model: intact recollection (indeed, better recollection than controls), but with notable impairments in familiarity.

Other evidence that recollection and familiarity rely on distinct structures in MTL comes from neuroimaging studies in healthy adults. Eldridge, Knowlton, Furmanski, Bookheimer, & Engel (2000) showed increased hippocampal activity at retrieval for old items given an R response in a Remember/Know task, while old items given a K response showed similar levels of hippocampal activity as misses and correct rejections, suggesting that the hippocampus contributes to recollection but not familiarity. Ranganath et al. (2004) later showed a double dissociation of activity at encoding, such that the hippocampus and posterior parahippocampal cortex were more active for words that were later recollected, defined as recognition with accurate source information, relative to items recognized without source memory. In contrast, rhinal cortex showed a graded pattern of activity that increased with higher confidence responses, consistent with familiarity, but no relationship with the accuracy of source recollection. A review by Eichenbaum, Yonelinas, and Ranganath (2007) found further evidence for this dissociation in MTL across a number of studies. They found that out of 19 contrasts examining recollection, as defined using either source recollection or R/K methods, 16 reported hippocampal activation, and 11 reported posterior parahippocampal activity, but only 2 reported anterior parahippocampal (perirhinal) activity. In contrast, of 15 contrasts examining familiarity, 13 showed perirhinal activity, while 4 showed activity in hippocampus, and 4 showed activity in posterior parahippocampal cortex.

Prefrontal activity is also important for memory, with partially separable contributions to recollection and familiarity. Early evidence (e.g., Jankowsky, Shimamura, & Squire, 1989) showed that patients with frontal lobe lesions were unimpaired when recalling semantic knowledge, but were impaired in source recall, suggesting a deficit specific to recollection. Knowlton and Squire (1995) showed in amnesiac patients that both recollection and familiarity rely on medial temporal lobe structures, contrary to earlier hypotheses, but also found evidence that recollection seems to rely on the frontal lobes, as the degree of frontal degeneration in Korsakoff's patients is associated with the severity of recollection impairment. Thus, they suggested that prefrontal processing is required, in addition to MTL-based mechanisms, for recollection but not familiarity.

Subsequent neuroimaging and lesion studies (e.g., Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Ranganath et al., 2004; Duarte, Ranganath, & Knight, 2005) have suggested, however, that prefrontal activity at encoding is important for both recollection and familiarity. These effects are partially distinct, but partially overlapping, for recollection and familiarity. For instance, Ranganath et al. (2004) reported greater activity in anterior portions of ventrolateral prefrontal cortex (VLPFC) during encoding of subsequently recollected items, while activity in frontopolar and medial orbital frontal cortex was associated with the strength of subsequent familiarity. Ranganath et al. found an additional area in posterior VLPFC (BA 44/6) to be associated with increases in both recollection and familiarity. Uncapher and Rugg (2005) found that activity during encoding in dorsal and posterior bilateral VLPFC was associated with Remember responses at both a short and long delay, while activity in a more ventral/anterior portion of VLPFC was associated with Remember responses only after a long delay. Know responses were associated with activity in precentral gyrus, with a combination of delay-invariant and short-delay specific effects. Thus, ventrolateral prefrontal activity during encoding, which has typically been associated with the controlled use of effective, deep encoding strategies (see Ranganath & Knight, 2003; Blumenfeld & Ranganath, 2007, for reviews) generally seems to lead either to increased recollection or to a combination of increased recollection and familiarity.

Relating dual process models to value-directed remembering

The series of studies reported presently are intended to further elucidate the encoding processes that differ as a function of value in the value-directed remembering paradigm, as well as to explore ways in which they may differ from the automatic, dopamine-driven reward-based learning manipulations that are more commonly found in the neuroscience literature (e.g., Adcock et al., 2006; Wolosin et al., 2012; Spaniol et al., 2014). Thus, one relevant question that should be considered is how manipulations that affect the depth of encoding processes differentially affect recollection and familiarity, as compared to how putatively dopamine-driven manipulations of item value at encoding affect these two processes.

One of the earliest studies to use the R/K paradigm (Gardiner, 1988) aimed to address this question, finding that deep processing at encoding led to increased Remember responses, relative to shallow processing, but there was no difference in Know responses. He also found a similar result when comparing generation to reading, another manipulation that should enhance the depth of encoding; generating led to a greater proportion of Remember responses, but no difference in Know responses. However, these results were based on raw proportions of R and K responses, and as noted above, there is reason to believe that the proportion of K responses in particular does not constitute a good estimate of familiarity.

When the Yonelinas and Jacoby (1995) correction is applied, or when other methods such as process dissociation or ROC analyses are used, the pattern of results is different. Specifically, Yonelinas (2002) found that across multiple studies, if independence is assumed, deep levels of processing and generation at encoding enhance both recollection and familiarity on a later test, albeit with a larger effect on recollection than on familiarity. In addition, as noted above, more recent studies (Brown & Bodner, 2011; Sheridan and Reingold, 2012) that have tried to separately assess recollection and familiarity without assuming independence have found strong evidence that items encoded on a deep level are more likely to be remembered than items encoded on a shallow level even if no episodic information is available. Thus, if value is affecting encoding processes in a similar way as would a level of processing manipulation, we would expect to see effects of value on both recollection and familiarity, at least in the context of an assumption that recollection and familiarity are independent processes, or in the context of a procedure in which recollection and familiarity are measured independently from each other.

In contrast to levels of processing, there are fewer studies that have examined how rewards that affect memory via dopamine-hippocampal interactions (e.g., Adcock et al., 2006) differentially enhance recollection and familiarity. However, the evidence that is available tends to suggest effects on recollection but not familiarity. Wittmann et al. (2005) tested effects of reward on incidental encoding, using a paradigm in which the reward is predicted by features of the cue stimulus (an image of a living or nonliving object), but reward is given based on performance on an unrelated task, and participants do not know that they will need to remember the cue. They found that the rates of remember responses and the rate of correct source judgments on a delayed memory test were higher for rewarded than unrewarded items; they also state that reward did not lead to increased familiarity, but do not show data on this point. They do, however, include fMRI data showing a value x subsequent memory interaction in dopamine-producing midbrain regions, and main effects of value and subsequent memory on hippocampal activity. As Wittmann et al. note, the importance of the hippocampus in both dopamine-driven memory enhancement and recollection leads to a natural prediction that reward, at least in an incidental learning paradigm like what they use, should selectively affect recollection.

A later behavioral study by Wittman, Dolan, & Düzel (2011) used word stimuli, and also showed that, at least when the aspect of the stimulus that is predictive of reward is also useful for enhancing memory, reward leads to an increase in Remember but not Know responses. In re-analyzing their raw data[7], it appears that there is no increase in the number of raw Know responses given to valued relative to non-valued items. However, it is less clear whether value has a beneficial effect on familiarity after correcting the proportion of Know responses for the proportion of recollected items. In their Experiment 1, using three levels of value, raw Know responses are clearly lower for valued items than non-valued items (see Wittmann et al., 2011). Even when the Yonelinas and Jacoby (1995) correction is applied, neither the medium (M = 21.3%) nor the high-value items (M = 31.1%) show a trend for greater corrected familiarity than the no-value items (M = 29.1%). Combining across medium and high-value groups, paired-samples t-tests show that value did have a reliable effect on recollection, $t(11) = 2.52$, $p = .029$, but not on familiarity, $t(11) < 1$. Although the interaction between the two effects is not statistically significant, $F(2, 22) = 2.69$, $MSE = 161.50$, $p = .129$, $\eta_p^2 = .196$, the apparent interaction appears relatively robust, and may only fail to reach significance due to the small sample size. Thus, the results from this experiment seem to support the conclusion that reward only affects recollection, and not familiarity, even when assuming independent processes.

However, Experiment 2 from Wittman et al. (2011), which used two rather than three levels of value but seems otherwise very similar to the experiment described above, is more equivocal on this point. Without applying the Yonelinas and Jacoby (1995) correction, there is a clear effect of value on Remember but not Know responses (see Figure 3 in Wittmann et al., 2011), and the trend for an interaction approaches significance, $F(1, 14) = 3.00$, $MSE = 98.34$, $p = .105$, $\eta_p^2 = .176$. When the correction is applied, however, familiarity estimates for rewarded items (M = 33.3%) tend to be higher than for non-

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[7] I thank Bianca Wittmann for providing raw data for this analysis.

rewarded items (M = 26.5%), and the difference approaches significance, $t(14)$ = 1.79, p = .095. While this effect is still numerically smaller than the analogous difference in recollection between rewarded (M = 21.8%) and non-rewarded (M = 12.8%) items, and the effect of value on recollection does reach significance, $t(14)$ = 2.23, p = .043, there is no statistical trend for an interaction between the two effects, $F(1, 14) < 1$. It is not clear why these results differ so strongly from Experiment 1 of the same study, but they do make it harder to draw an unequivocal conclusion about whether reward leads to increased familiarity.

Recent preliminary results by Gruber and colleagues (Gruber et al., 2014b; Gruber, Yonelinas, & Ranganath, 2015) provide some additional evidence to support the idea that encoding-related manipulations that enhance memory via reward-related activation selectively improve recollection. Specifically, Gruber et al. (2014b) presented participants with short blocks of stimuli, each of which began with a cue for high or low reward value, presented together with a question, e.g., “Heavier than a basketball?”, intended to evoke incidental deep encoding of the stimuli to follow. Four pictures displaying concrete objects were then shown in each block, about which participants answered the given question. A background scene was also incidentally presented throughout each block. Reward feedback was given at the end of each block based on the accuracy of responses to the question, i.e., not based on memory for the item. After this incidental encoding task, memory was tested using a modified R/K procedure, allowing either a subjective judgment that the item was recollected, or a rating of confidence from 1-5 for items that were not recollected. Individual pictures in high-reward blocks were more likely to produce recollection relative to low-reward blocks, but the proportion of items yielding confident familiarity-based memory did not differ as a function of reward.

Gruber et al. (2015) found a similar result using a somewhat different task. They presented participants with questions about which that individual either was or was not curious, and tested memory for faces that were incidentally presented after each trivia question. Previously, Gruber et al. (2014a) showed that individual differences in memory for such faces correlated with the strength of the curiosity x subsequent memory interaction in bilateral substantia nigra (SN)/ventral tegmental area (VTA) and right hippocampus, as well as with the degree of functional connectivity between left SN/VTA and left hippocampus. The curiosity-driven improvement in memory for these faces thus seems to be mediated by interactions between activity in dopaminergic reward-sensitive regions and hippocampus, analogous to what has been shown previously with incidental encoding in the context of monetary reward (e.g, Wittmann et al., 2005). Gruber et al. (2015) replicated the behavioral finding that incidental encoding of faces was stronger when the question preceding the face is one about which the participant was curious, but also found that this manipulation specifically enhanced recollection of items, but not familiarity-based memory, using the same modified R/K procedure as that used by Gruber et al. (2014b). In a second experiment by Gruber et al. (2015), incidentally-encoded memoranda included both a face and a background scene. In that experiment, curiosity did not reliably affect the ability to recognize presented faces in terms of either recollection or familiarity. However, memory for the association between the face and the background scene, i.e., accurate source memory, was better for high-curiosity items, while the rate of accurate item memory with incorrect source context did not differ by curiosity condition.

Thus, this experiment as well suggests an enhancement of recollection by curiosity, but no corresponding effect on familiarity.

Although these data are limited by small sample sizes, and have not yet been peer-reviewed, they do provide us with some basis for believing that the finding of benefits to both recollection and familiarity in Exp. 2 of the Wittmann et al. (2011) study was an outlier. In other words, it seems reasonable to assume that under incidental learning conditions, automatic memory enhancement mediated by increased activity in reward-sensitive regions prior to encoding will typically lead to an improvement in recollection but not familiarity.

Finally, an fMRI study by Shigemune, Tsukiura, Kambara, & Kawashima (2014) showed effects of value on recollection but not familiarity in an intentional encoding paradigm. Specifically, memory for source details (specifically, the side of the screen on which a to-be-learned word was presented) was enhanced for items in which correct recognition responses could lead to earning a reward, or could lead to avoiding punishment, relative to non-rewarded items. There was no effect of reward or punishment on the proportion of items recalled correctly without accurate source information, which can be considered a measure of familiarity. Neuroimaging results confirmed that dopaminergic reward regions were more active during rewarded and punished items, relative to neutral, that the hippocampus was more active during encoding for items in which source was successfully recalled, and that dopaminergic reward regions and hippocampus show enhanced functional connectivity when encoding items for which both item and source retrieval would be accurate later. These results provide further evidence favoring our assumption that activation of the dopaminergic reward system, which mediates automatic, non-strategy-driven improvement of memory for high-value items, specifically improves recollection of those items, but tends not to affect familiarity.

Aging

Finally, it is important to consider how the various manipulations described here are affected by aging. A number of reviews and meta-analyses (e.g., Light, Prull, LaVoie, & Healy, 2000; Yonelinas, 2002; Prull, Dawes, Martin, Rosenberg, & Light, 2006; Koen & Yonelinas, 2014) have found that older adults show consistently and substantially reduced recollection compared to young adults. For familiarity, deficits related to aging tend to be weaker than those found for recollection, and evidence is mixed as to whether aging leads to a decrease in familiarity at all. Koen and Yonelinas found that studies using an R/K procedure show an effect of age on familiarity estimates, corrected for independence, while studies using a process dissociation procedure or ROC method do not, on average, find reliable decrements in familiarity with normal aging. Prull, Dawes, Martin, Rosenberg, & Light (2006) took a different approach to comparing methods, collecting data from the same set of subjects using R/K, process dissociation, and ROC methods, all tested on different days. They found effects of age on recollection via all 3 methods, while also finding an age-related decrease in familiarity via the R/K and ROC methods, but did not find such a decrease using the process dissociation method. One possible explanation for these differences is that older adults tend to apply subjective ratings such as remember/know in a different way than do young adults. In any case, we can conclude that the ability to discriminate old from new items on the basis of familiarity is at least partially, and maybe entirely, preserved in healthy older adults.

Other work has shown that older adults tend to have trouble spontaneously initiating effective encoding mechanisms, but when the study environment makes it easier for them to do so, memory can be substantially improved, particularly recollection. Perfect, Williams, & Anderton-Brown (1995) tested both old and young adults in an R/K paradigm, with items varied using a levels of processing manipulation. After correcting their reported raw proportions using the Yonelinas and Jacoby (1995) formula, it appears that older adults show a substantial benefit for deep processing on recollection, but no benefit for familiarity; in contrast, young adults showed increases in both recollection and familiarity for deeply-processed items.

Another relevant study, by Luo, Hendriks, & Craik (2007), aimed to clarify findings from an earlier review by Craik and Jennings (1992), which had found that interactions between age and encoding manipulations were inconsistent, while using a process dissociation procedure to examine how these manipulations separately affect recollection and familiarity. When to-be-studied nouns were presented in picture form, older adults showed a greater improvement in memory than young adults, relative to a verbal baseline condition. Luo et al. suggest that this result is due to the picture condition making it easier for older adults to use imagery-based encoding processes, a strategy that older adults are less likely to apply spontaneously than young adults. Comparing process estimates, the picture condition led to increased recollection in both age groups, relative to baseline. Although overall recollection estimates were still somewhat lower in older adults, older adults also tended to have a larger increase in recollection relative to baseline, compared to young adults, in this condition. Older adults also showed greater familiarity estimates than did young adults in the picture condition. When a generation strategy was used, older adults showed a similar improvement in recollection as compared to young adults, while not affecting familiarity in either age group. Luo et al. describe generation as a beneficial encoding strategy that neither young adults nor older adults would typically apply spontaneously, and thus it should help both about equally. Finally, a third strategy, imagining a sound effect to go with the word, increased recollection for young adults, but did not help older adults; here, the learner needs to self-generate a mental scaffolding for the manipulation to be helpful, which is more difficult for older adults. The sound effect manipulation also did not affect familiarity estimates. The primary conclusion from this study as it applies to our work is that encoding manipulations that improve memory in older adults generally do so by improving recollection, helping to rectify the deficit normally found in this component of memory. However, enhanced familiarity is also possible, in addition to improved recollection, with encoding manipulations that are particularly beneficial for older adults.

The present studies

In the work described here, we examine how value-directed remembering separately enhances recollection and familiarity. We do so in young adults via three different methods: ROC analysis, remember/know judgments, and task dissociation. While Experiments 2-6 only test healthy young adults, we do report data from one group of older adults in Experiment 1B, which can provide some preliminary data regarding how value-related differences in encoding affect memory in a dual-process context. Another major theme of the work contained herein is how features of the VDR paradigm, particularly the inclusion of multiple study-test cycles with feedback, leads to the unique pattern of brain activity discussed in prior chapters, which is distinct from the dopamine-driven memory enhancement often examined in neuroscience studies. One interesting possibility is that both recollection and familiarity will be enhanced for high-value items when people get practice and feedback with intervening free recall tests, while only recollection will be enhanced when such practice and feedback is not available. If such a dissociation is present, we would expect to see it in the experiments described here.

Experiment 1A

Our first attempt to examine how value differentially influences recollection and familiarity came from a follow-up analysis of data that was collected as part of the fMRI experiment reported in Chapters 2 and 3. In brief, we presented a recognition test with 6 levels of confidence following the MRI scan, about 30-60 minutes after initial learning of the words. We then used the Dual Process Signal Detection model (Yonelinas, 1994) to generate estimates of recollection and familiarity for high-value and low-value items for each participant. In addition to examining the behavioral data on its own, it is also possible to examine how value-related differences in brain activity during encoding predict value-related differences in the dual process measures that we discuss here, to potentially find additional effects of value in the brain that did not emerge when using selectivity on the free recall test as our behavioral measure.

Method

Participants. Of the 20 young adults who participated in the MRI study initially reported in Chapter 2, 19 participants (M_{age} = 21.21 years, SD = 3.17 years, range = 18-30 years, 10 female, 9 male) contributed data to this experiment (one individual did not complete this portion due to experimenter error).

Materials and Procedure. After completing the value-directed remembering task described in Chapter 2, each participant completed a version of the monetary incentive delay (MID) task in the scanner (Knutson, Adams, Fong, & Hommer, 2001), which lasted about 10 minutes counting instructions, followed by 14 minutes of structural scans. After emerging from the scanner and getting resettled, which took between 5 and 20 minutes, participants were presented with a recognition test. The test included 240 words, each presented one at a time, self-paced. These items consisted of the 120 words presented in the scanner (60 high-value, 60 low-value), and an equal number of lure words that met the same psychometric criteria as the original items. Participants were to respond to each word with one of six levels of confidence (1 = definitely new, 2 = probably new, 3 = maybe new, 4 = maybe old, 5 = probably old, 6 = definitely old).

For the ROC analysis, we computed the proportion of items at or above each of the 6 levels of confidence, for high-value old items, low-value old items, and new items, and generated separate ROC curves comparing high-value old items to new items, and low-value old items to new items. We used the DPSD solver template provided on the Yonelinas lab web site (http://yonelinas.faculty.ucdavis.edu/software/), in combination with the Microsoft Excel Solver, to produce estimates of recollection and familiarity for high-value items and low-value items. We also ran the same analyses using only old items that were not recalled on the free recall tests, for reasons that will be discussed further below.

For fMRI data analysis, procedures were generally the same as described in Chapters 2 and 3. One difference is that, in order to be more comprehensive about ROI analyses while not sacrificing statistical power, correction for multiple comparisons is not applied universally here, as it is not always clear what could constitute a similar group of

ROIs, and how strict it is necessary to be. However, key results that would clearly not survive correction for multiple comparisons across a particular group of ROIs are noted as such.

Results

Analysis of raw confidence ratings. We first examine effects of value on raw confidence ratings. Paired-samples t-tests confirm that mean confidence ratings were higher for high-value items ($M = 5.48$, $SD = 0.45$) than for low-value items ($M = 4.36$, $SD = 0.77$), $t(18) = 6.14$, $p < .001$. In addition, mean confidence ratings for new items ($M = 2.53$, $SD = 0.70$) were less than mean ratings for either high-value items, $t(18) = 13.23$, $p < .001$, or low-value items, $t(18) = 7.00$, $p < .001$. Thus, as was apparent in the free recall data (see Chapter 2), memory for high-value items was reliably better than memory for low-value items on the recognition test, but both high-value and low-value items were remembered significantly better than items that were not studied at all.

One potential complication in interpreting results from the post-scan recognition test is that recollection may be enhanced further for items that were recalled, due to memory for the recall test itself rather than due to processes that happened during encoding. Because more high-value items were recalled than low-value items (see Figure 2.2), this outcome would create a bias in favor of finding stronger memories for high-value items. Thus, we ran all analyses in two ways: once with all items, and again using only non-recalled items, that is, words that were not recalled on the free recall test. Analyses run only on non-recalled items may also be problematic, as this approach excludes all of the items that were encoded most strongly, potentially biasing the analysis too much towards items that are more weakly encoded. Still, we can be confident that any effects that are consistently found across both approaches would have been present regardless of any contamination from the free recall test. A different approach to addressing this potential problem is described in Experiment 5.

When examining only non-recalled items, the effects of value on mean confidence ratings are consistent with what was described above. That is, high-value items (M = 4.76, SD = .66) are remembered more strongly than low-value items (M = 3.93, SD = .81), $t(18)$ = 3.72, p = .002. Still, memory strength was lower for non-studied items (M = 2.53, SD = .70) than for both high-value old items, $t(18)$ = 9.55, $p < .001$, and low-value old items, $t(18)$ = 6.18, $p < .001$. Thus, even when looking only at items that were not recalled, items associated with high point values were remembered better than low-value items, but items in both categories were remembered better than non-studied items.

Another way of examining how value and true memory status affected recognition responses is by examining the distribution of responses for high-value old, low-value old, and new items. From a visual examination of Figure 4.1, it is clear that most high-value old items are rated as old with high confidence, both when considering all items (Figure 4.1A)

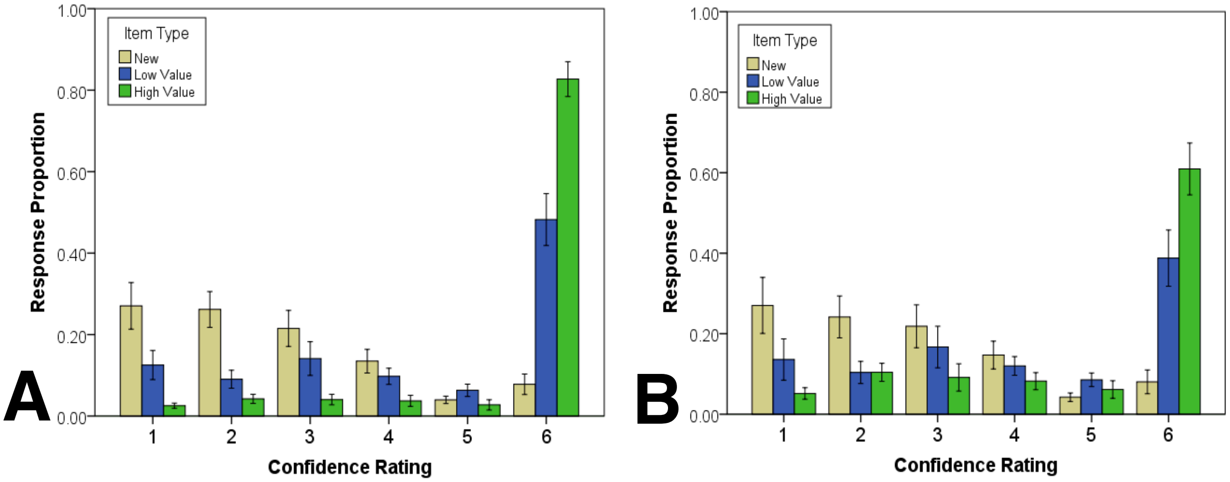

Figure 4.1. Proportion of high-value old items, low-value old items, and new items given responses at each of confidence, counting (A) all items, and (B) only non-recalled items, in young adults in Experiment 1A. Error bars represent +/- 1 SE.

and when recalled items are excluded (Figure 4.1B). A majority of low-value old items were also rated as old with high-confidence, although a paired-samples t-test confirms that the rate of high-confidence old ("6") responses is reliably higher for high-value items than for low-value items, for all items, $t(18) = 6.76$, $p < .001$, and also for non-recalled items, $t(18) = 4.75$, $p < .001$. High-confidence old responses were significantly more likely for high-value old items than for new items, looking at all items, $t(18) = 17.42$, $p < .001$, and at non-recalled items, $t(18) = 11.92$, $p < .001$. High-confidence old responses were also significantly more likely for low-value old items than for new items, for all items, $t(18) = 7.18$, $p < .001$, and for non-recalled items, $t(18) = 6.45$, $p < .001$. Less-confident "probably old" responses ("5") were more common for low-value than high-value items when considering all items, $t(18) = 3.32$, $p = .004$, but this effect is not reliable when looking only at non-recalled items, $t(18) = 1.52$, $p = .146$. This response type is also more common for low-value items than for new items, examining all items, $t(18) = 2.32$, $p = .032$, and examining only non-recalled items, $t(18) = 3.05$, $p = .007$. However, there is no difference in the number of "probably old" responses between high-value items and new items, either for all items, $t(18) = 1.36$, $p = .192$ or for non-recalled items, $t(18) < 1$. The lowest-confidence old ("4") responses were also more common for low-value old items than for high-value old items, for all items, $t(18) = 3.75$, $p = .001$ and for non-recalled items, $t(18) = 2.23$, $p = .039$. However, these responses were reliably less common for low-value than for new items across all items, $t(18) = 2.69$, $p = .015$, with a marginal effect in the same direction in non-recalled items, $t(18) = 1.93$, $p = .07$. Finally, "4" responses were also less common for high-value old items than for new items, both for all items, $t(18) = 4.08$, $p = .001$, and for non-recalled items, $t(18) = 2.76$, $p = .013$.

We also examine effects of encoding condition on the summed proportion of responses from the 3 levels of confidence (1, 2, and 3) that reflect a belief that an item was new. New items are significantly more likely to be rated as new than are items from either category of old items. Specifically, when all items are analyzed, new items are more likely to be rated as new than high-value old items, $t(18) = 14.40$, $p < .001$, and low-value old items, $t(18) = 6.93$, $p < .001$. Similarly, when only non-recalled items are analyzed, new items are more likely to be rated as new, compared to high-value old items, $t(18) = 10.30$, $p < .001$, and compared to low-value old items, $t(18) = 5.81$, $p < .001$. In addition, low-value items were significantly more likely to be rated as new than low-value items, for all items, $t(18) = 5.87$, $p < .001$, and for non-recalled items, $t(18) = 3.43$, $p = .003$.

ROC analysis. Fitting the behavioral data using a dual-process signal detection model (Yonelinas, 1994) allows for a more meaningful way to summarize the results. Before describing the results of this analysis, it should be noted that there are two potential limitations that can require subjects to be excluded from this analysis. First, if there is not enough variability in the responses provided, such as if all or nearly all items are given an extreme confidence rating of either “1” or “6”, it is not possible to compute stable ROC estimates. In this experiment, one individual was excluded from all ROC analyses due to this limitation, as this person never used intermediate levels of confidence. When we repeated the analyses using only non-recalled items, it was necessary to exclude three additional subjects who had fewer than 5 non-recalled high-value old items, as stable ROC estimates cannot be computed with such a small number of old items.

When considering all items, we find higher mean recollection estimates for high-value items than for low-value items, $t(17) = 6.89$, $p < .001$, but familiarity estimates do not differ as a function of value, $t(18) < 1$ (Figure 4.2A). A 2 x 2 (process x value) within-subjects ANOVA does not find an interaction between these factors, however, $F(1, 18) = 2.17$, $MSE = .26$, $p = .159$, $\eta_p^2 = .11$. We find similar results when only non-recalled items are considered: estimates of recollection are significantly higher for high-value items, $t(14) = 3.96$, $p = .001$, but estimates of familiarity do not differ for high vs. low-value items, $t(14) < 1$ (Figure 4.2B). The interaction is not significant here either, however, $F(1, 18) = 3.08$, $MSE = .40$, $p = .101$, $\eta_p^2 = .18$. Thus, it seems that high-value items are more likely to be recollected than low-value items, even if they were not recalled on the initial free recall test.

There is no evidence to support value-directed modulation of encoding activity having a beneficial effect on subsequent familiarity. However, it actually seems that performance on this test was dominated almost entirely by recollection, so there is little ability to detect any effects on familiarity that could be present. Specifically, when all items are considered, familiarity estimates do not differ reliably from zero, either for high-value

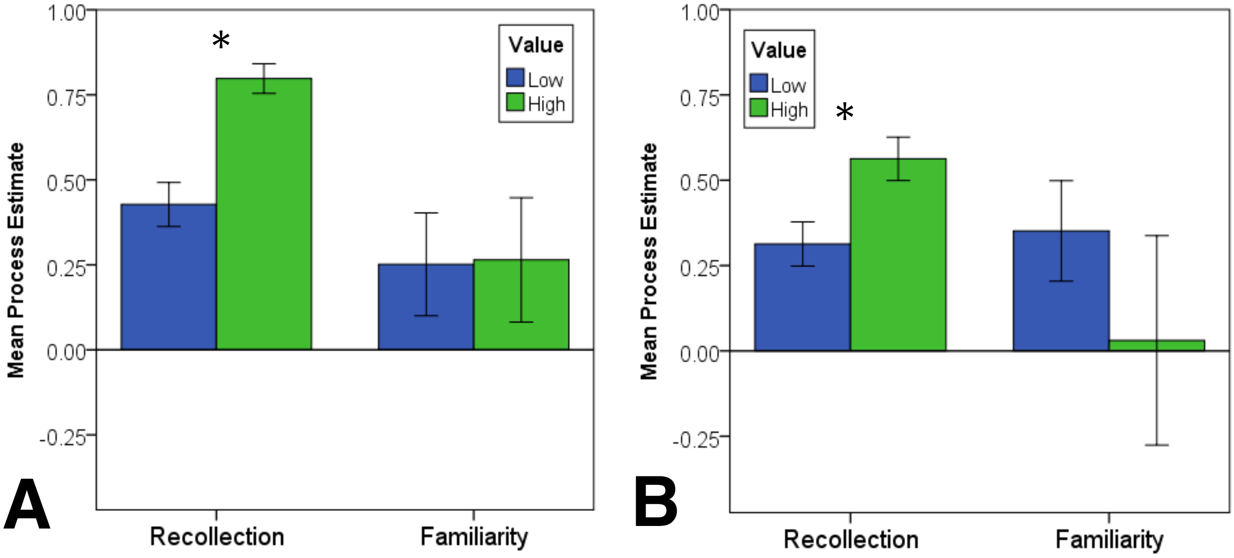

Figure 4.2. Mean process estimates derived from ROC curves in young adults in Exp. 1A, considering (A) All items, (B) Non-recalled items. Error bars represent +/- 1 SE.

items, $t(17) = 1.45$, $p = .166$, or for low-value items, $t(17) = 1.66$, $p = .114$. When only non-recalled items are considered, familiarity estimates again do not differ from zero for high-value items, $t(17) < 1$, but are reliably above zero for low-value items, $t(17) = 2.39$, $p = .031$. Thus, it is not possible to rule out the idea that value could enhance the ability to remember items using familiarity when recollection fails. Later experiments will clarify this issue.

Neural correlates. Because these data were collected in the context of a neuroimaging study, it is also possible to relate the strength of value effects during the post-scan recognition test back to the fMRI data collected during encoding. A whole brain analysis shows that the difference in estimated recollection for high-value vs. low-value items correlates with value-related differences in brain activity during the word-encoding period in the left ventrolateral prefrontal cortex (VLPFC; peak voxel: -50, 38, 10; Figure 4.3A). The positive effect looks quite similar to the prefrontal effect that emerges when value-related differences in brain activity during word encoding are correlated with selectivity on the immediate free recall test (compare to Figure 2.4). Additionally, there is a

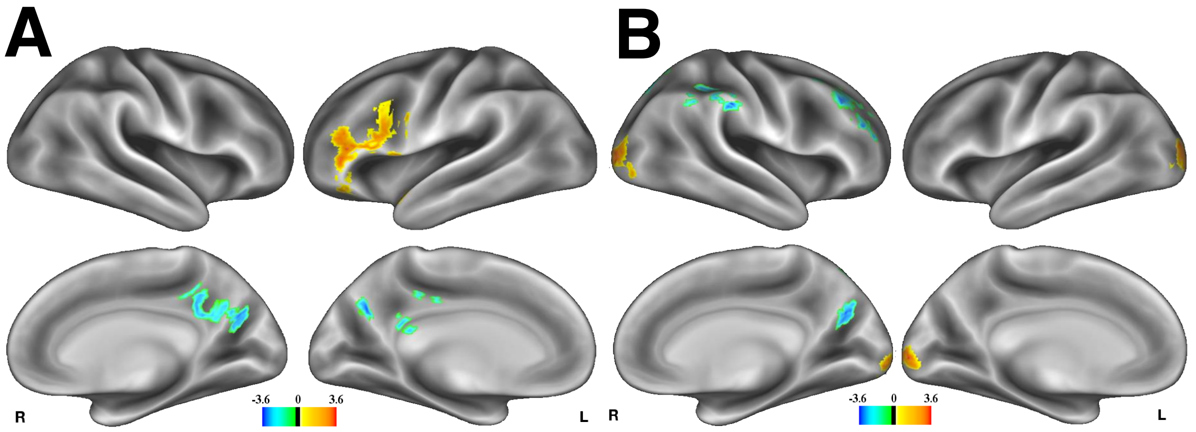

Figure 4.3. Brain-behavior correlation between effects of value on brain activity during the word-encoding period and effects of value on recollection estimates on the subsequent recognition test in young adults in Experiment 1A. Process estimates were computed using (A) all items, and (B) non-recalled items.

cluster in medial posterior parietal cortex, specifically precuneus and posterior cingulate, in which value-related differences in brain activity during word encoding negatively correlate with value-related differences in recollection (peak voxel: -2, -66, 32).

As with the behavioral results, it is also important to examine whether these effects replicate when only non-recalled items are used to compute recollection estimates. One way to do this is to extract the cluster that emerged from the previous whole-brain analysis as a region of interest. When doing so, we find that the left VLPFC cluster that showed a positive brain-behavior correlation with recollection estimates computed using all items (as shown in Figure 4.3A) is no longer significant when only non-recalled items are used to compute recollection estimates, $r = .35$, $p = .20$. While a correlation analysis between this ROI and the original behavioral measure is not valid due to circularity, it is informative to compare the circularly-defined correlation coefficient computed using recollection estimates from all items to the analogous correlation with recollection estimates defined using only non-recalled items, using a test of dependent correlation coefficients (Steiger, 1980). Doing so indicates that the correlation using only non-recalled items is significantly reduced as compared to the correlation computed using all items for the same 15 participants ($r = .69$), $t(13) = 2.45$, $p = .029$. Using a similar approach on the cluster that showed a negative brain-behavior correlation, we find that the correlation in that cluster remains significant when only non-recalled items are included, $r = -.56$, $p = .030$. This correlation coefficient does not differ from that obtained when using all items to compute recollection estimates ($r = -.66$), $t(13) < 1$. Thus, it seems that at least some portion of the positive effect of value-related modulation of left VLPFC activity on recollection estimates is due to items that were recalled on the free recall test, and this effect is no longer reliable when those items are removed. By contrast, the negative effect, whereby greater deactivation of posterior midline regions on high-value items leads to greater value-related differences in recollection, appears to hold true regardless of whether recalled items are included in the analysis.

Another way to address the issue of how recalled items may be contaminating the analysis in some way is to repeat the whole-brain analysis using recollection estimates computed using only non-recalled items. When doing this (Figure 4.3B), we see some brain-behavior correlations that are similar to what emerge when all items are included, but also some notable differences. Most notably, as may be expected based on the preceding analysis, there is no positive effect in left VLPFC, or in any other regions related to semantic processing. Here, the only regions showing positive correlations between value-related differences in activity during encoding and differences in recollection were in bilateral occipital cortex (peak voxels: L occipital lobe, -10, -98, 4; R occipital lobe, 16, -94, 0). However, we do still see a negative correlation in R precuneus (peak voxel: 12, -66, 54), as well as in R dorsolateral PFC (peak voxel: 46, 40, 26) and R supramarginal gyrus (peak voxel: 44, -40, 50).

During the cue period, the only region in which effects of value on recollection reliably correlated with differences in brain activity was in a small cluster in right occipital cortex, which showed a positive brain-behavior correlation (peak voxel: 18, -92, 2). A similar effect was also observed when only non-recalled items were used to compute process estimates (peak voxel: 14, -94, 4). We also examined whether there were any brain regions in which value-related differences in familiarity estimates correlated with effects of value in the brain, during either the cue period or the word-encoding period. No significant clusters emerged from these whole-brain analyses. These results reinforce the conclusion that, in young adults, value-related differences in performance on the post-scan recognition test are largely driven by value-related changes in encoding processes that specifically lead to enhanced recollection for high-value items.

ROI analyses. A region of interest (ROI) analysis is also useful in order to both clarify and extend the findings from the whole-brain analysis. First, we look at ROIs related to semantic processing, to determine whether stronger value-related modulation of semantic processing during encoding leads to greater value-related differences recollection, as was suggested by the whole-brain analysis. The three ROIs used for this analysis are the Neurosynth-derived semantic network ROI, described in Chapter 3 (see Figure 3.5), and the more focal L BA 45/47 and L BA 44/6 ROIs initially described in Chapter 2. During the word period, effects of value on activity in the Neurosynth semantic network ROI correlate with effects of value on estimates of recollection, $r = .48$, $p = .046$, but not with effects of value on familiarity, $r = .31$, $p = .206$. The analogous correlations during the cue period were not significant either for recollection, $r = .29$, $p = .249$, or for familiarity, $r = .17$, $p = .496$. In the more focal L BA 45/47 prefrontal ROI initially described in Chapter 2, we again see a trend towards a correlation between value-related modulation of brain activity during the word-encoding period and value-related differences in recollection on the recognition test, $r = .47$, $p = .050$, but no correlation with effects of value on familiarity, $r = .36$, $p = .137$. However, in this ROI, we also find an intriguing effect during the cue period, as value-related differences in brain activity are significantly correlated with value-related differences in recollection, $r = .48$, $p = .043$, but not with value-related differences in familiarity estimates, $r = .17$, $p = .506$. These effects do not replicate in the more posterior L BA 44/6 prefrontal ROI; effects of value during the word period show a marginal trend towards a correlation with effects of value on recollection, $r = .44$, $p = .070$, but the analogous effect during the cue period is not significant, $r = .23$, $p = .363$, nor is the correlation with familiarity significant during either temporal period, all $|r| < .14$.

Similar to what emerged from the whole-brain analysis, these ROI effects are notably weaker when only non-recalled items are used to compute the behavioral measures. Indeed, value-related differences in recollection no longer significantly correlate with value-related differences in brain activity during the word-encoding period in any of the semantic processing ROIs: Neurosynth semantic network, $r = .38$, $p = .17$; L BA 45/47, $r = .25$, $p = .369$; or L BA 44/6, $r = .06$, $p = .84$. The only one of these coefficients that is significantly reduced compared to the analogous correlation computed based on all items is in BA 44/6, $t(13) = 2.22$, $p = .045$, and the correlation in that ROI was only marginally significant even when all items are included. There are also no reliable correlations between recollection and activity during the cue period in any of these ROIs: Neurosynth semantic network, $r = .33$, $p = .231$, L BA 45/47, $r = .43$, $p = .111$, or L BA 44/6, $r = -.15$, $p = .583$. Interestingly, however, value-related differences in familiarity, as estimated using non-recalled items, do correlate with activity in semantic ROIs. Specifically, there is a significant correlation in the L BA 45/47 ROI, $r = .57$, $p = .025$, and a marginal effect in the Neurosynth semantic network ROI, $r = .50$, $p = .058$, with no trend towards an effect in L BA 44/6, $r = .24$, $p = .40$. While the significant correlation here would not survive correction for multiple comparisons, and should thus be interpreted cautiously, these findings are intriguing, and suggest that during encoding of items for which recall will ultimately fail, increased brain activity related to semantic processing may lead to increases in familiarity-based recognition instead.

In addition to ROIs related to semantic processing, we also examine whether effects of value in ROIs related to reward correlate with effects of value on recollection and familiarity estimates. As noted in Chapter 3, it was somewhat surprising that the large value-related modulation of reward-processing regions during the cue did not correlate with selectivity during free recall. This part of the study uses a recognition test, however, as well as a somewhat longer delay, both of which may make the dopaminergic mechanism driven by activity in the midbrain and ventral striatum more relevant. However, here again, we do not find a correlation between effects of value during the cue period in the Neurosynth-derived reward ROI (see Figure 3.8) and value-related differences in either recollection, $r = .18$, $p = .467$, or familiarity, $r = .03$, $p = .90$. We also do not find such a correlation in the more focal atlas-derived NAcc ROI described in Chapter 3, either for recollection, $r = .18$, $p = .465$, or for familiarity, $r = .08$, $p = .758$. Finally, somewhat contrary to what we found when looking at selectivity in free recall, we also do not find correlations between value-related modulation of activity in either ROI during the word period and effects of value on either recollection or familiarity estimates, all $|r| < .27$, $p > .28$. When process estimates derived from the non-recalled subset of items are used, we also do not find any significant correlations in either reward ROI, all $|r| < .32$, $p > .24$.

Finally, given the negative subsequent memory effects that emerged from the whole-brain analysis, we also generated ROIs based on the meta-analysis by Kim (2011). The three regions that seem most relevant based on the whole-brain analyses shown in Figure 4.3 are R precuneus, R temporoparietal junction (TPJ), and R superior frontal gyrus

(SFG). When all items are included in the analysis, there are trends towards negative correlations between effects of value in the brain during the word period in these regions and effects of value on recollection, but these are at best marginally significant, in R precuneus, $r = -.41$, $p = .088$, in R TPJ, $r = -.44$, $p = .065$, and in R SFG, $r = -.39$, $p = .111$. Effects during the cue period are not significant, all $|r| < .30$, $p > .234$. However, when the behavioral measures are computed based on non-recalled items, we do find significant negative correlations during the word period in R precuneus, $r = -.62$, $p = .013$, and in R SFG, $r = -.72$, $p = .002$, but no reliable correlation in R TPJ, $r = -.38$, $p = .161$. Surprisingly, there is a positive correlation between effects of value on recollection and activity in R TPJ during the cue period, $r = .55$, $p = .034$; the analogous correlations are not reliable in R SFG, $r = .34$, $p = .216$, or in R precuneus, $r = .19$, $p = .50$, however. There are also no significant correlations with familiarity in these ROIs, during either the cue period or the word period, regardless of whether all items or non-recalled items are analyzed. There may be trends toward negative correlations with familiarity during the word period when all items are included, particularly in R precuneus, $r = -.39$, $p = .106$, or R SFG, $r = -.35$, $p = .156$, but these effects are not significant, and all other $|r| < .32$, $p > .200$. Thus, it does seem that, at least when the behavioral measure is computed based on non-recalled items, value is modulating negative subsequent memory effects in similar brain regions to where those effects have previously been shown.

Discussion

It appears that whatever young adults are doing differently to strengthen encoding of high-value items, they are largely strengthening the recollection component of memory. Even when recalled items are removed from the behavioral analysis, there is still a robust effect of value on estimates of recollection as determined by ROC curves. The fMRI results obtained when recollection estimates are computed based on all items are also consistent with the interpretation that value-related modulation of encoding activity, particularly in prefrontal regions related to semantic processing, enhances subsequent recollection.

However, the failure to replicate the correlation between effects of value on brain activity in semantic processing regions and effects of value on recollection estimates from the non-recalled subset of items, and the fact that in some regions related to semantic processing, the correlation was reliably weaker when recalled items were excluded from the analysis, leaves open the possibility that the brain-behavior correlations that we observe when all items are included are at least partially mediated by effects on free recall. In other words, given that individuals who have greater differences in encoding-related activity in VLPFC also have a greater advantage for high-value items on the free recall test (see Chapter 2), and some recollection-based responding on the recognition test may reflect memory for the recall test itself, we cannot be sure that modulation of VLPFC activity at encoding directly enhances recollection on the recognition test.

The negative correlations between effects of value during encoding and effects of value on recollection are also notable. A number of prior studies (e.g., Otten & Rugg, 2001; Daselaar, Prince, & Cabeza, 2004; Park & Rugg, 2008; Kim, 2011; Mattson, Wang, de Chastelaine, & Rugg, 2014) have found that greater deactivations relative to baseline in regions similar to those shown in Figure 4.3 are found for subsequently remembered vs. subsequently forgotten items. It seems likely that these deactivations reflect deactivation of default-mode network regions. Default-mode regions are generally deactivated during performance of demanding cognitive tasks, and reduced activity typically reflects reduced attention to internally-directed cognitive processes, and increased focus on the task at hand (e.g., Buckner, Andrews-Hanna, & Schacter, 2008). Both the whole-brain results and the ROI analyses based on activation peaks from the meta-analysis by Kim (2011) suggest that the degree to which people selectively deactivate default-mode network regions during encoding has a strong impact on how much value affects recollection on the later memory test. Given that the effects in semantic processing regions are only present when both recalled and non-recalled items are included in the memory measures, while these negative subsequent memory effects, if anything, get stronger when recalled items are excluded from those measures, it is possible that the continued effect of value on recollection that is present in the behavioral data for non-recalled items is being driven by how strongly people deactivate default-mode regions during encoding. Further work would be necessary to confirm this explanation, however.

Both the behavioral and neuroimaging data are inconclusive as to whether value-based modulation of encoding activity enhances familiarity. In the behavioral data, when looking at all items, there is a trend for high-value items to yield somewhat higher estimates of familiarity, but this trend reverses when recalled items are removed from the analysis, and in any case, it is not close to being statistically significant in either case. In the neuroimaging data, the apparent trends are for effects of value on familiarity to correlate positively with effects of value on brain activity in semantic processing regions, particularly when recalled items are excluded from the analysis, and possibly also to correlate negatively with activation in default mode network regions. These effects would be consistent with high value enhancing familiarity via similar mechanisms as how it enhances recollection, but again, the trends are weak and merely suggestive. Thus, further experiments will be necessary to better address whether high-value items encoded in the value-directed remembering paradigm show only enhanced recollection, or whether these items show an enhancement in both recollection and familiarity.

The significant correlation between effects of value on recollection and brain activity during the cue period in L BA 45/47 deserves some discussion as well. Although this effect would not survive a Bonferroni-Holm correction for multiple comparisons across the three ROIs tested, and thus must be interpreted cautiously, it may help to address one of the key issues raised in Chapter 3. Specifically, we noted that young adults tend to more strongly engage brain areas related to both semantic processing and reward during high-value cues, relative to low-value cues, despite the fact that such modulation of brain activity does not seem to affect performance in our free recall task. The finding described here suggests that, in line with prior literature (e.g., Otten et al., 2006; Addante et al., 2015), the degree of proactive engagement of prefrontal brain regions does correlate with the degree of enhanced recollection for high-value items at a 30-60 minute delay, even among a group of subjects who distinctly did not show a benefit for such proactive activation in an immediate free recall task.

Experiment 1B

Another important question to be addressed in this series of studies is how encoding in the value-directed remembering paradigm separately affects recollection and familiarity in older adults. As noted above, older adults tend to be particularly impaired on tests of recollection relative to young adults, but encoding manipulations that improve memory in older adults tend to strengthen recollection, reducing this impairment. At the same time, some manipulations that improve encoding processes in older adults seem to enhance familiarity as well as recollection (e.g., Luo et al., 2007). Given that familiarity is relatively preserved in older adults, we might indeed expect that some manipulations of encoding will be effective largely because they lead older adults to draw more on familiarity mechanisms that are preserved with aging, rather than recollection mechanisms that are degraded. The present experiment tested older adults using the exact same paradigm as Experiment 1A.

Methods

Participants. This experiment was conducted as part of the older adult fMRI study described in Chapter 3. Recognition data were not available for two participants, leaving 21 individuals (M_{age} = 68.05 years, *SD* = 5.56 years, range = 60-80 years, 13 female, 8 male) for this part of the study.

Materials and Procedure. The materials and procedure were identical to that described in Experiment 1A. Note that one individual in the older adult group apparently reversed the response scale, so responses were reverse-scored for that individual.

Results

Raw confidence ratings. We first analyze how item status at encoding affected recognition ratings, with all items included in the analysis. Paired-samples t-tests confirm that, like young adults, older adults gave reliably higher ratings for high-value items (M = 5.09, SD = .73) than for low-value items (M = 4.18, SD = 1.07), $t(20) = 5.61$, $p < .001$. In addition, older adults could reliably distinguish old items from new items (M = 2.59, SD = .88), both for high-value old items, $t(20) = 11.13$, $p < .001$, and for low-value old items, $t(20) = 5.47$, $p < .001$. Results are similar when only non-recalled items are included in the analysis. High-value items (M = 4.51, SD = .95) were still recalled significantly better than low-value items ($M = 3.93$, $SD = 1.00$), $t(20) = 3.36$, $p = .003$. Non-recalled old items were still given significantly higher ratings than new items, whether for high-value items, $t(20) = 7.81$, $p < .001$, or for low-value items, $t(20) = 5.47$, $p < .001$.

We can also examine the distribution of responses across the different confidence levels. Visual examination of Figure 4.4A shows a largely similar distribution of responses as what we found in young adults in Experiment 1A. Looking at all items, we find that high-confidence old ("6") responses made up a greater proportion of responses to high-value old items than to low-value old items, $t(20) = 5.11$, $p < .001$. The proportion of high-confidence old responses was consistently greater for old items than for new items, whether the old items were high-value, $t(20) = 12.85$, $p < .001$, or low-value, $t(20) = 5.87$, $p < .001$. At the next lowest level of confidence, "probably old" ("5"), there was a marginal effect such that low-value items tended to have a higher response proportion than high-value items, $t(20) = 1.78$, $p = .09$. Neither group of old items differed from new items at this level of confidence, $ts < 1.18$. The next lowest level of confidence, "maybe old" ("4"), was reliably more likely

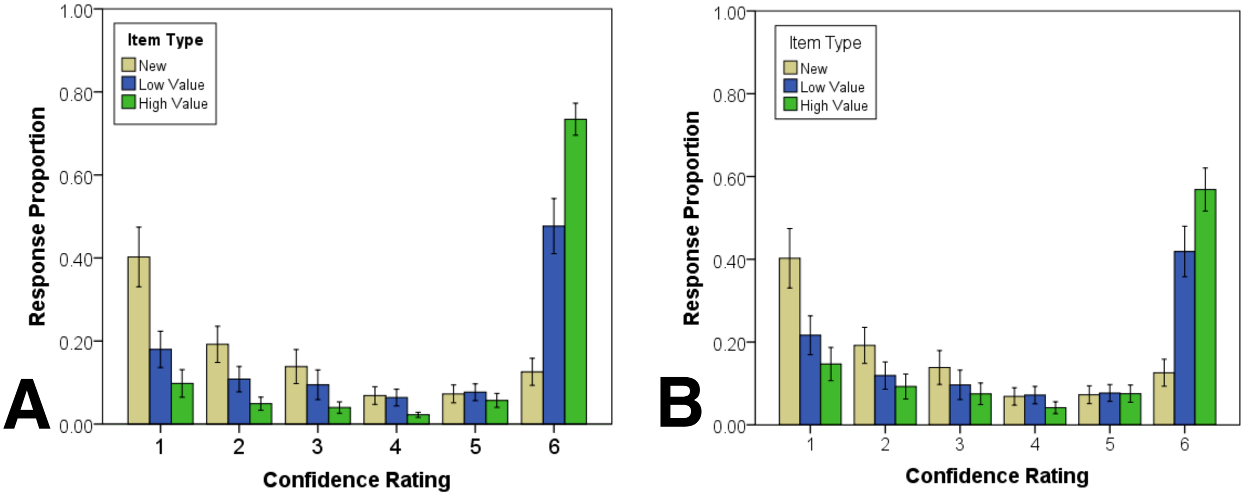

Figure 4.4. Proportion of high-value old items, low-value old items, and new items given responses at each of confidence, counting (A) all items, and (B) only non-recalled items, in older adults in Experiment 1B. Error bars represent +/- 1 SE.

for low-value items than high-value items, $t(20) = 2.24$, $p = .037$. This response was also more likely for new items than high-value items, $t(20) = 2.34$, $p = .030$, but was equally likely for low-value old items and new items, $t(20) < 1$. Finally, combining across all 3 levels of confidence for new responses, we find that "new" responses were significantly more likely for low-value old items than for high-value old items, $t(20) = 5. 30$, $p < .001$. Still, "new" responses were more likely to be given on new items, relative to high-value old items, $t(20) = 11.31$, $p < .001$, and low-value old items, $t(20) = 5.87$, $p < .001$.

Patterns were again largely similar when we perform the same analysis only on non-recalled items (Figure 4.4B). High-value old items were more likely to be recognized with high confidence ("6") than low-value old items, $t(20) = 4.01$, $p = .001$. Still, high-confidence old responses were significantly less likely for new items than for either high-value old items, $t(20) = 8.82$, $p < .001$, or low-value old items, $t(20) = 5.73$, $p < .001$. There were no reliable differences between item types for the likelihood of choosing a "probably old" ("5") response, all ts < 1, nor were there any reliable effects of item type on the likelihood of choosing a "maybe old" ("4") response, all ts < 1.52. Finally, again combining across the three levels of "new" responses, we find that "new" responses were significantly more likely for low-value items than for high-value items, $t(20) = 3.93$, $p < .001$, but were also significantly more likely for new items than for either high-value old items, $t(20) = 8.02$, $p < .001$, or low-value old items, $t(20) = 5.87$, $p < .001$. Thus, it is clear that older adults were able to discriminate old from new items at both value levels, even when recalled items are removed from the analysis.

ROC analysis. To gain a more fine-grained understanding of how value affects memory on the recognition test, we generated ROC curves for each individual subject, and examined how the estimates of recollection and familiarity differ across value conditions. Two individuals who had fewer than five responses at intermediate levels of confidence for at least one ROC plot (high-value old vs. new, and/or low-value old vs. new) were excluded from all analyses of the ROC data, as these individuals would not have enough variability to allow computation of stable ROC estimates. In the remaining 19 subjects, we find that high-value items produce both greater recollection, $t(18) = 3.38$, $p = .003$, and greater familiarity, $t(18) = 3.06$, $p = .007$, relative to low-value items (Figure 4.5A). The process x value interaction is not significant, $F\,(1, 18) = 2.04$, $MSE = .20$, $p = .171$, $\eta_p^2 = .102$, but the trend suggests, if anything, a larger effect of value on familiarity than on recollection. That trend becomes even more distinct when we only examine non-recalled items (Figure 4.5B). For this analysis, two additional individuals were excluded, one whose process estimates were nonsensical for high-value non-recalled items (recollection = -12.81), and another who had fewer than 5 high-value non-recalled items. For the remaining 17 subjects, we find that recollection estimates are equivalent across value groups, $t(16) = 1.13$, $p = .277$,

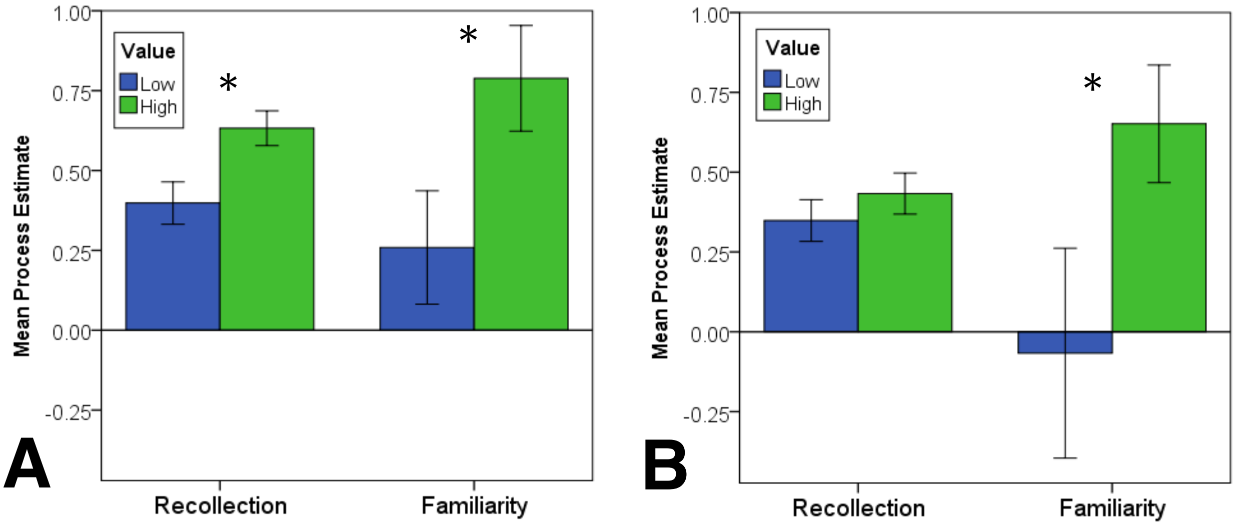

Figure 4.5. Mean process estimates derived from ROC curves in older adults in Experiment 1B, considering (A) All items, (B) Non-recalled items. Error bars represent +/- 1 SE.

but familiarity was still greater for high-value items than for low-value items, *t*(16) = 2.37, *p* = .031. The process x value interaction was marginal for this analysis, *F*(1, 16) = 3.29, *MSE* = .52, *p* = .089, η_p^2 = .17. These results indicate that when recalled items are excluded from the analysis, there is no residual effect of value on recollection of non-recalled items as there was in young adults, but value still has a strong effect on familiarity.

Whole brain analysis—Recollection. Older adults show a number of brain regions in which value-related differences in activity during the word-encoding period correlate with value-related differences in recollection during the recognition test. A whole-brain analysis (Figure 4.6) reveals left-lateralized activations in left VLPFC (peak voxel: -48, 10, 30), left inferior lateral temporal cortex (peak voxel: -54, -66, -2), and left occipital cortex (peak voxels: -24, -90, -4; -10, -108, -10). No such effects are apparent during the cue period.

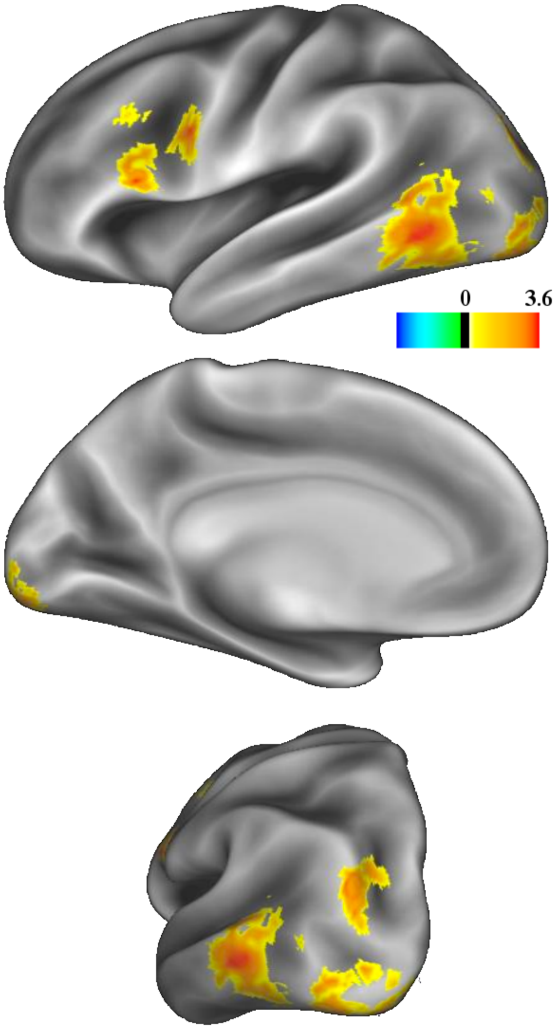

Figure 4.6. Regions showing correlations between effects of value on brain activity during the word-encoding period and effects of value on recollection estimates on the subsequent recognition test, with process estimates computed using all items. All reliable effects are in left hemisphere, so only this hemisphere is shown here.

Using the same approach as in Experiment 1A, we examined whether brain-behavior correlations in these same clusters are reliable, as well as whether they are significantly reduced, when only non-recalled items are used to compute recollection estimates. Indeed, we find that there is no longer a significant effect in the left VLPFC cluster shown in Figure 4.6 under these conditions, $r = -.02$, $p = .93$, and this effect is significantly weaker than the circularly-defined effect obtained using all items ($r = .71$), $t(15) = 5.79$, $p < .001$. Similarly, the L lateral temporal effect is not significant here, $r = .34$, and this effect is also significantly weaker than the circularly-defined effect using all items ($r = .89$), $t(15) = 5.17$, $p < .001$. Finally, combining the two L occipital clusters into a single ROI, we find that this cluster also is not significant when only non-recalled items are used, $r = .23$, $p = .381$, and the effect with non-recalled items is again significantly lower than that obtained using all items ($r = .75$), $t(15) = 3.34$, $p = .004$.

We did also run a whole-brain analysis using recollection estimates computed on the basis of non-recalled items alone as the behavioral measure, correlated with value-related differences in brain activity during the word-encoding period (Figure 4.7). Here, we find a significant cluster in left lateral temporal cortex (peak voxel: -50, -62, 2), similar to that obtained with all items, and we also find a significant effect in right occipital cortex

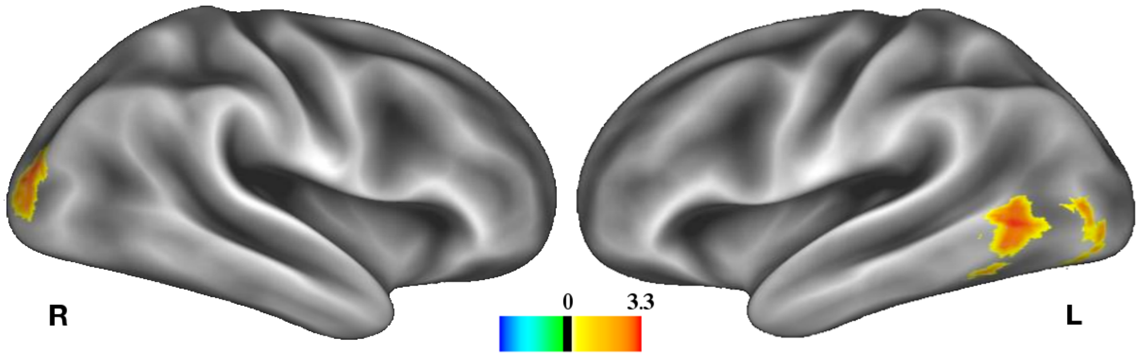

Figure 4.7. Regions showing correlations between effects of value on brain activity during the word-encoding period and effects of value on recollection estimates on the subsequent recognition test, when process estimates are computed using only non-recalled items.

(peak voxel: 36, -88, 14). However, as in young adults, there is no reliable correlation in left VLPFC in this version of the analysis. No reliable brain-behavior correlations emerged from a similar analysis looking at brain activity during the cue period.

ROI analyses—Recollection. We also examine how value-related differences in brain activity in the independently-defined ROIs discussed in earlier chapters relate to value-related differences in subsequent recollection. When using all items to compute recollection estimates, we find strong positive correlations in all three semantic processing-related ROIs: in the Neurosynth semantic network ROI, $r = .56$, $p = .012$, in the L BA 45/47 prefrontal ROI, $r = .48$, $p = .036$, and in the L BA 44/6 prefrontal ROI, $r = .68$, $p < .001$. None of these three regions show such correlations during the cue period, all $|r| < .28$, $p > .247$. Additionally, none of the effects found during the word period survive when only non-recalled items are used to compute recollection estimates. Specifically, brain-behavior correlations during the word period in the Neurosynth semantic ROI, $r = -.02$, $p = .94$, in the L BA 45/47 ROI, $r = -.24$, $p = .35$, and in the L BA 44/6 ROI, $r = -.03$, $p = .92$, were not significant. Each of these effects is significantly smaller than the analogous effect when recollection estimates are computed using all items, across this same subset of subjects: Neurosynth semantic ROI, $t(15) = 4.70$, $p < .001$, L BA 45/47 ROI, $t(15) = 4.48$, $p < .001$, and L BA 44/6, $t(15) = 5.79$, $p < .001$ all $t(15) > 4.48$, $p < .001$. It seems clear that greater activity during the word-encoding period in semantic processing regions does predict increased recollection on the recognition test when all items are considered. However, as was the case for young adults, we cannot rule out the possibility that these correlations are mediated by effects of value on the earlier free recall test.

In addition to the effects in semantic processing regions, we also find a positive correlation between value-related changes in brain activity in at least one reward-sensitive region during the cue period and effects of value on recollection computed using all items. Specifically, such a correlation is apparent in the focal NAcc ROI, $r = .53$, $p = .019$. The correlation is not reliable in the larger Neurosynth-derived reward network ROI, however, $r = .34$, $p = .159$. It also is not present for activity during the word period, either in the NAcc ROI, $r = .25$, $p = .307$, or in the Neurosynth reward ROI, $r = .35$, $p = .143$. We did not find such an effect in young adults, nor was such an effect apparent in the analysis of free recall data reported in Chapter 3 in older adults. Still, the cue period effect in NAcc suggests that, at least in older adults, the added delay, and the need to use recollection in a somewhat different way than on a free recall task, may be sufficient to allow some dopamine-driven reward effects to emerge on the recognition test.

As in the semantic processing ROIs, the correlation between effects of value on recollection and value-related differences in brain activity in NAcc during the cue period is not significant when recollection estimates are computed using only non-recalled items, $r = .09$, $p = .73$. The difference between this effect and the analogous finding computed using all items is marginally significant, $t(15) = 1.90$, $p = .077$. No other correlations with reward ROIs during either the cue period or the word period are significant in the analysis using only non-recalled items, all $|r| < .26$, $p = .317$. Thus, the cue period reward effect observed above may also be driven by items that were recalled on the free recall test. However, unlike the effects in semantic processing regions during the word period, there was not an analogous correlation between value effects on brain activity during encoding and selectivity index during free recall. Thus, even if the correlation is being driven by items that were recalled during the initial free recall test, it is less likely that this effect is being driven by memory for the free recall test itself, as compared to the effects in semantic processing brain regions.

We also examine whether there were any negative subsequent memory effects on recollection in older adults in the right-hemisphere precuneus, TPJ, and SFG ROIs defined above. There was a marginal negative correlation in R precuneus during the word period when only non-recalled items were included in the behavior measure, $r = -.46$, $p = .061$, which would replicate one of the effects found in young adults. No other effects were apparent in any of these 3 ROIs, however, during the cue period or during the word-encoding period, using all items or using only non-recalled items, all $|r| < .27$, $p > .269$. Thus, deactivation of default-mode regions seems to have much less of an effect, if any, on subsequent recollection in older adults, as compared to young adults.

Age differences—Recollection. Finally, in order to see how the brain-behavior correlations between effects of value on brain activity during encoding and effects of value on recollection differ for young vs. older adults, we ran a whole-brain comparison across age groups, using the procedure described in Chapter 3. When recollection estimates are computed based on all items, we find a cluster in right precuneus (peak voxel: 16, -62, 32) in which the negative brain-behavior correlation in precuneus in young adults is reliably different than the analogous brain-behavior correlation in older adults (Figure 4.8A). In addition, this same analysis shows a small cluster in left ventral occipital cortex (peak voxel: -16, -98, -8) in which older adults show a stronger positive brain-behavior correlation effect than young adults (Figure 4.8B). When the analysis is run again using recollection estimates computed from non-recalled items, we find four clusters in which young adults show reliably stronger effects than older adults (Figure 4.8C). In two clusters, in right occipital cortex (peak voxel: 28, -96, 8) and left occipital cortex (peak voxel: -28, -94, 12), young adults show stronger positive brain-behavior correlation effects than do older adults. Two other clusters emerge in which young adults show negative brain-behavior correlations that are reliably different than the analogous effects in older adults: one in right precuneus (peak voxel: 20, -62, 24), and the other in right DLPFC (peak voxel: 42, 40, 30). The most notable finding here is that the tendency for young adults, but not older adults, to show correlations between the

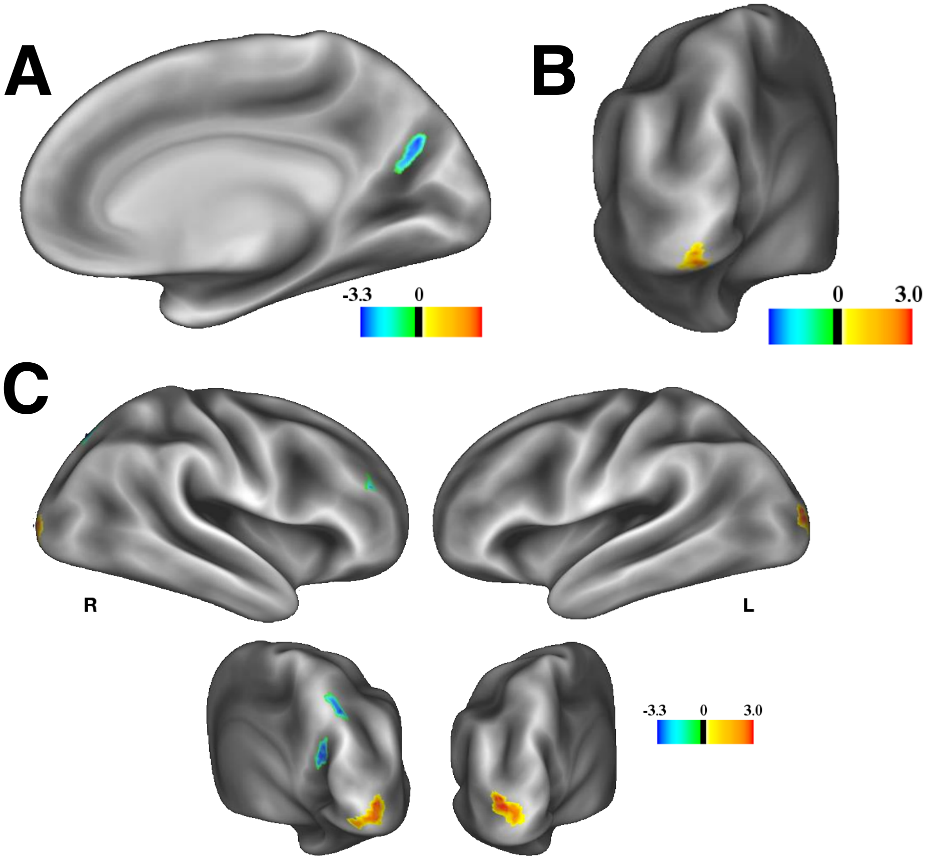

Figure 4.8. Regions showing age differences in correlations between value-related differences in brain activity during the word-encoding period and value-related differences in recollection. (A) Analysis using all items to compute recollection estimates, showing a significant deactivation in right precuneus that is reliably larger in young adults. (B) Same analysis as A, but showing a positive brain-behavior correlation effect in left occipital cortex that is stronger in older adults. (C) Brain-behavior correlation when only non-recalled items are used to compute recollection estimates, showing both positive and negative brain-behavior correlations that are significantly stronger in young adults.

degree of deactivation in default-mode network regions and effects of value on recollection in the later recognition test is supported by a significant difference between age groups.

Neural correlates—Familiarity. There is, however, another way in which brain activity during encoding affects recognition in older adults. Specifically, it appears that value-related differences in activity during the word encoding period are negatively correlated with value-related differences in familiarity in a bilateral network of posterior medial brain regions, including bilateral precuneus/occipital cortex (L peak voxel: -12, -66, 62; R peak voxel: 16, -62, 4), R lateral occipital cortex (peak voxel: 42, -

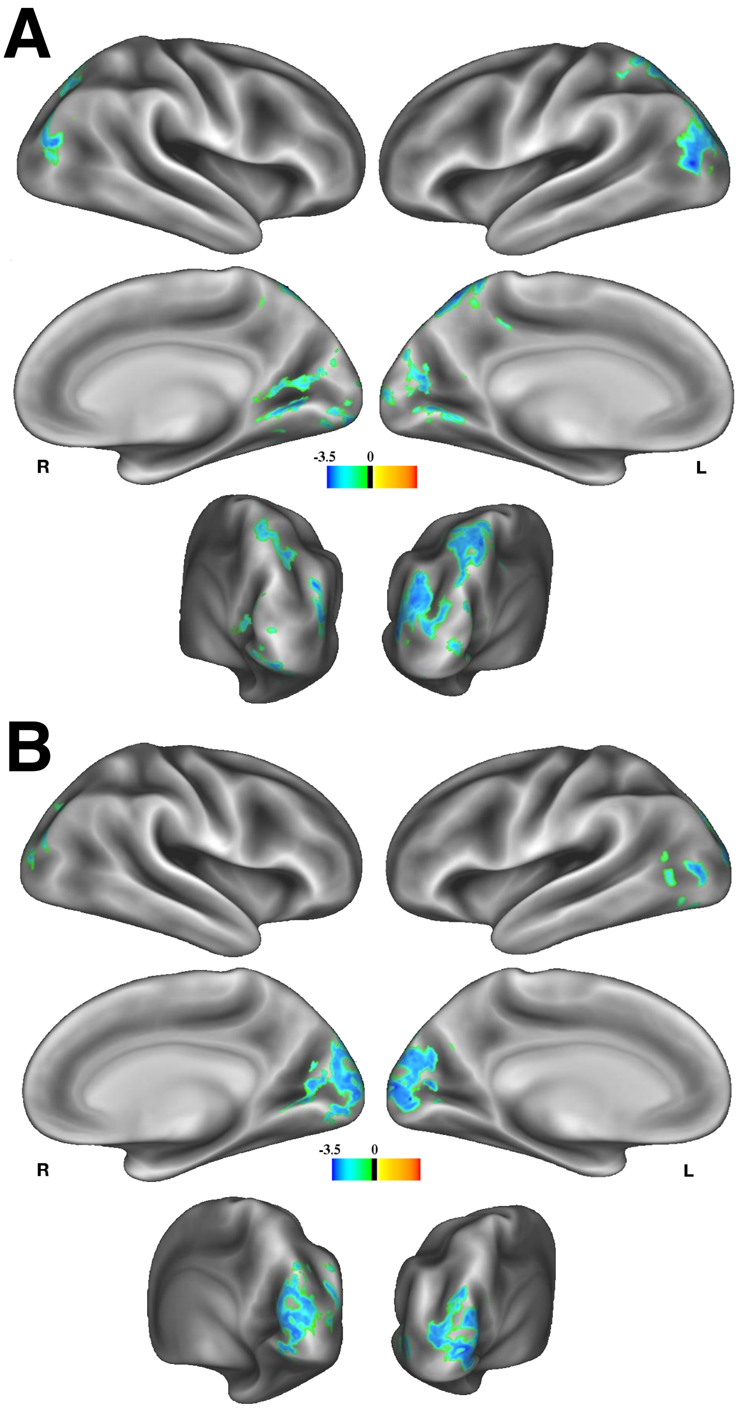

Figure 4.9. Brain-behavior correlation analysis showing regions in which age-related differences in activity during the word-encoding period as a function of value correlate with value-related differences in familiarity estimates, when those estimates are calculated based on (A) all items, and (B) non-recalled items alone.

74, 16), and L posterior cerebellum (peak voxel: -26, -74, -24) (Figure 4.9A).

Following the procedure described above to determine whether this effect is being driven by items that were recalled in the earlier free recall test, we extracted as ROIs the clusters that showed this effect, and correlated the mean parameter estimates from within those clusters with value-related differences in familiarity estimates computed based only on non-recalled items. We find that one largely right-lateralized cluster that extends through medial occipital cortex and ventral precuneus shows a correlation of almost equal magnitude with non-recalled items, $r = -.67$, $p = .003$, compared to the circularly-defined correlation computed based on all items ($r = -.75$), $t(17) < 1$.

By contrast, in a more dorsal parietal cluster, which is largely left-lateralized, and includes superior parietal lobule and precuneus, the correlation is not significant with non-recalled items, $r = -.22$, $p = .396$, and this effect is significantly weaker than the correlation with all items ($r = .71$), $t(17) = 4.38$, $p < .001$. Similarly, the correlations in R lateral occipital cortex, $r = -.16$, $p = .53$, and in L cerebellum, r = -.05, $p = .85$, are weaker than the analogous correlations computed using all items, both $t > 4.00$, $p < .001$. Thus, it seems that the brain-behavior correlation in some of the regions that appear in Figure 4.9A are being driven by items recalled on the free recall test, but the effects in medial occipital and ventral precuneus are still reliable when only non-recalled items are analyzed.

Consistent with these results, we find that the network that emerges from a whole-brain correlation analysis for which the behavioral measure was computed using only non-recalled items (Figure 4.9B) is partially similar to that obtained with all items. The largest cluster is in bilateral medial occipital cortex (peak voxel: -4, -98, 14), with another cluster in left lateral temporal cortex (peak voxel: -48, -76, 8); in this analysis, there are no clusters in dorsal precuneus or superior parietal lobule. Thus, it seems that at least some portion of these effects is independent of free recall. Note also that these effects only emerge during the word-encoding period, as no significant effects emerge from the whole-brain analysis during the cue period.

Age differences—Familiarity. As noted above, there were no correlations between effects of value on familiarity and brain activity in young adults. Thus, it is also important to determine whether there is a reliable age difference in this effect. A whole-brain analysis shows that indeed, there is a cluster in the left superior parietal lobule/precuneus (peak voxel: -10, -60, 62) in which the negative correlation between value effects on familiarity, computed based on all items, and value-related differences in brain activity is significantly stronger in older adults than in young adults (Figure 4.10A). When familiarity estimates are computed based on non-recalled items (Figure 4.10B), there is also a region in which older adults show a greater negative correlation between brain activity during encoding and familiarity, but it is located more ventrally, in occipital cortex (peak voxel: -2,

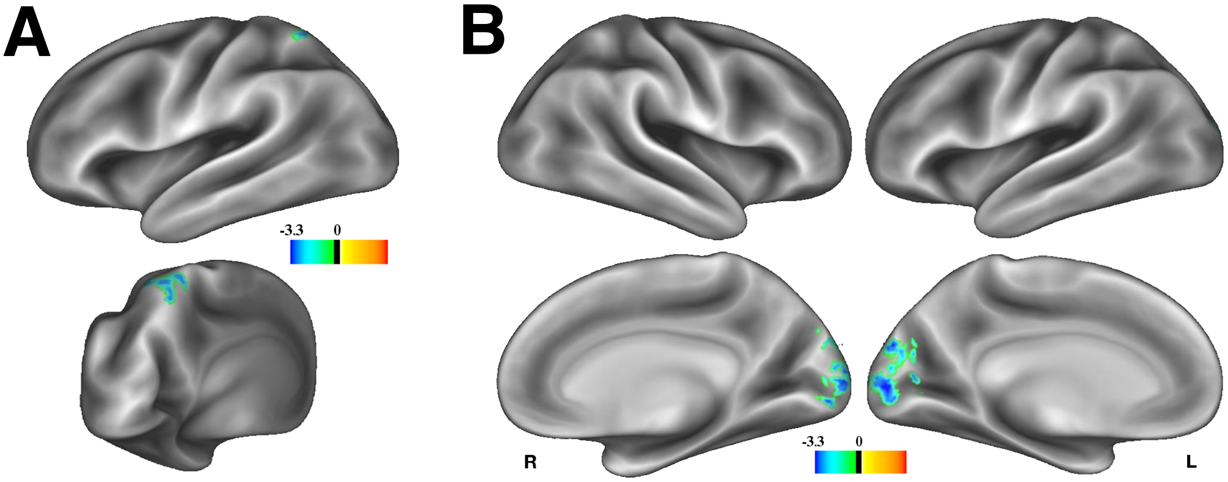

Figure 4.10. Regions in which negative brain-behavior correlations between effects of value during the word encoding period in the brain and effects of value on familiarity are reliably stronger in older adults. Process estimates are computed using (A) all items, and (B) non-recalled items.

-86, 32).

These effects are in the same general vicinity as the negative subsequent memory effects that relate to recollection in young adults, and as have been found in prior studies, but they seem to be shifted to some degree compared to the effects shown by others. Indeed, the effects described in this section are not reliably present in any of the three ROIs described above from the meta-analysis by Kim (2011), regardless of whether process estimates are computed using all items or only non-recalled items, all $|r| < .40$, $p > .111$. However, one recent study did find a negative subsequent memory effect in left precuneus that overlaps in part with the effects that we see when all items are used to estimate familiarity. That study (Mattson et al., 2014) examined negative subsequent memory effects in both young and older adults, while also separating item memory, which is believed to be based largely on familiarity, from source memory, which is largely driven by recollection. The relevant analysis looked at age-dependent subsequent memory effects, and found four clusters with age-dependent effects on item memory, in which young adults, but not older adults, showed reduced activity when the item was remembered. The L dorsal precuneus peak from that analysis overlaps not only with the correlation in older adults shown in Figure 4.9A, but also with the cluster showing a significant age x value interaction in Figure 4.10A.

ROI analyses. An ROI analysis using a sphere with radius 8 mm, centered on the L dorsal precuneus peak reported by Mattson et al. (2014), confirms that the older adults in our study showed a significant negative correlation between effects of value on brain activity in that area during the word encoding period and effects of value on familiarity, $r = -.54$, $p = .017$. Trend-level negative correlations with familiarity were also apparent in spherical ROIs centered on two of the other three peaks from the Mattson et al. study showing age-dependent effects on item memory, in R dorsal precuneus, $r = -.45$, $p = .052$, and in L TPJ, $r = -.43$, $p = .068$. The only one of the 4 ROIs from this set to not show at least a marginal trend towards a negative correlation with effects of value on familiarity was centered on the more ventral R precuneus peak, $r = -.06$, $p = .83$. This also was the only one of these 4 ROIs to show a significant negative correlation with effects of value on recollection in young adults, $r = -.49$, $p = .040$, underscoring the separability of negative subsequent memory effects on recollection in young adults and negative subsequent memory effects on familiarity in older adults. Finally, we also find no correlation in older adults between effects of value on familiarity and brain activity in an ROI centered on midcingulate cortex, $r = .05$, $p = .83$, which was the only region in which Mattson et al. found negative subsequent memory effects that were age invariant for young and older adults, confirming that it is the regions showing age-dependent effects in their study that seem to be most relevant here. Note that none of the correlations with familiarity described here are significant when only non-recalled items are examined, meaning that the effects may be driven by items that were recalled on the free recall test. Still, even if that is the case, these effects were not apparent in the brain-behavior correlations with free recall data itself. Thus, it seems that the effects are still novel even if they are only apparent when recalled items are included in the analysis.

It is also notable that in the L precuneus ROI showing the strongest negative correlation with familiarity, the corresponding correlation for recollection is nearly significant in the positive direction, $r = .45$, $p = .055$, and this correlation is significantly different from the correlation for familiarity, $t(19) = 3.03$, $p = .008$. The corresponding correlation between effects of value in this ROI and recall selectivity for the same group of subjects is also significant in the positive direction, $r = .51$, $p = .026$, which again differs significantly from the correlation with familiarity, $t(19) = 3.58$, $p = .002$. This point will be addressed further below, but the results suggest that brain-behavior correlations with recollection vs. familiarity in older adults are, to some degree, in opposition to each other.

We also repeat the ROI analyses that were described above in the context of recollection to determine how value-related differences in familiarity correlate with activity in semantic processing regions. None of the three semantic processing-related regions show significant correlations between value-related activity during the cue or word period of the encoding task and differences in familiarity, even as estimated using all items. There is a marginal negative correlation in the Neurosynth semantic processing ROI during the word period, $r = -.44$, $p = .060$, and other such correlations during both the word period and the cue period trend in a negative direction, but none of those approach significance, all $|r| < .32$, $p > .178$. There are significant negative correlations in the reward ROIs, however. Specifically, value-related differences in activity in the Neurosynth reward ROI during the word encoding period show a significant negative correlation with effects of value on familiarity, $r = -.48$, $p = .037$, and the analogous correlation in the NAcc ROI is marginal, $r = -.45$, $p = .052$. Additionally, there is a marginal negative correlation with familiarity in the NAcc ROI during the cue period, $r = -.45$, $p = .052$, while the analogous correlation in the Neurosynth reward ROI during the cue period is not significant, $r = -.33$, $p = .162$. These effects are not found when only non-recalled items are used to compute familiarity estimates, all $|r| < .26$, $p > .317$. Thus, in brain regions related to semantic and reward processing, in addition to in L precuneus, it appears that effects of value on brain activity correlate in opposite directions with recollection and familiarity, with greater activity tending to both enhance effects of value on recollection and dampen effects of value on familiarity.

Recollection-Familiarity differences. To further explore the extent of this pattern, we computed two separate z-scores for each participant, one reflecting value-related differences in recollection and the other reflecting value-related differences in familiarity, relative to other subjects in the same age group. The difference between these scores could be used as a relative measure of how much value affected recollection vs. familiarity for a given individual. While value-related differences in recollection vs. familiarity were not significantly correlated with each other in either age group, it is notable that the

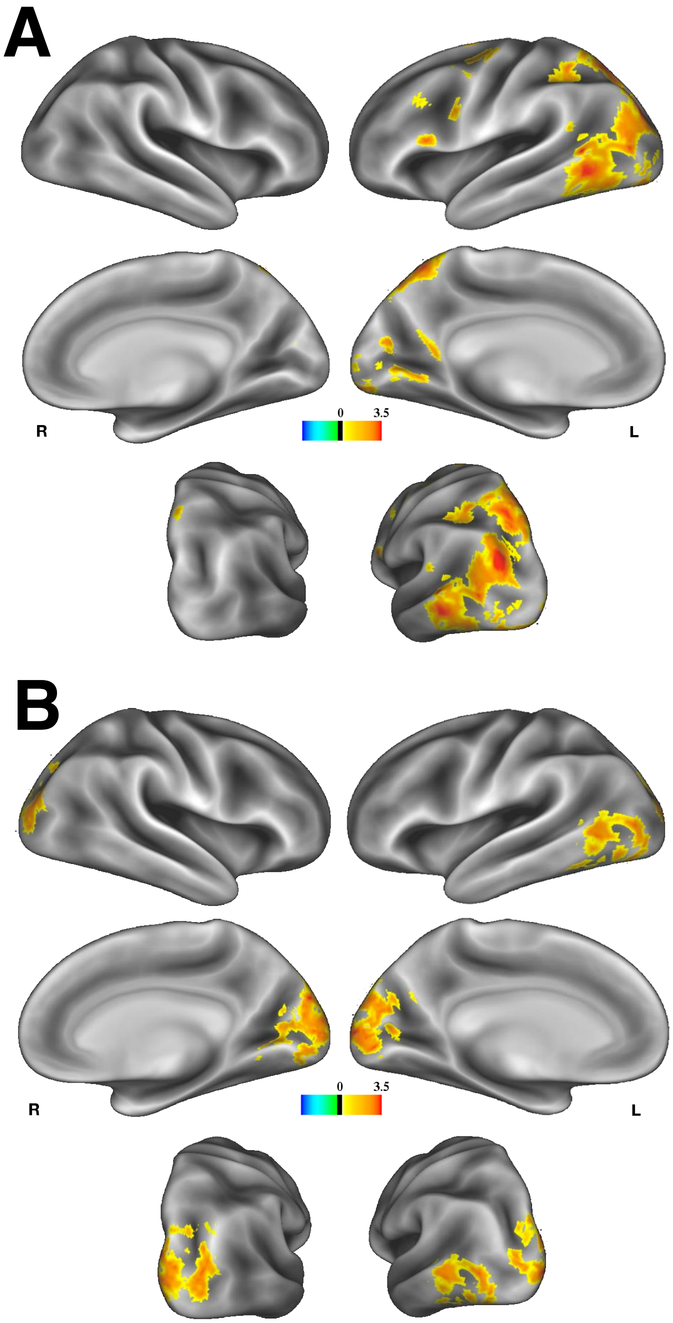

Figure 4.11. Regions in older adults showing a significant positive correlation with the difference in value effect z scores between recollection and familiarity. In areas showing this effect, increased activity leads to relatively greater recollection but relatively lower familiarity for high-value items. Process estimates are computed using (A) all items, and using (B) non-recalled items.

trend was positive in young adults, *r* = .20, *p* = .42, but was negative for older adults, *r* = -.34, *p* = .156.

We were then able to run a brain-behavior correlation analysis using this difference score as our behavioral measure. In young adults, there are no significant clusters that correlate with this measure, during either the word-encoding period or during the cue period. In older adults, however, there are a number of regions in which increased activity during the word-encoding period as a function of value correlates with the difference between effects of value on recollection and familiarity. A whole-brain analysis (Figure 4.11A), using process estimates computed using all items, finds one large cluster (peak voxel: -32, -86, 28), largely left-lateralized, spanning L occipital cortex, L posterior lateral temporal cortex, L superior parietal lobule, and bilateral dorsal precuneus. Additional clusters are also found in L inferior frontal gyrus (peak voxel: -56, 16, 22), L inferior occipital cortex (peak voxel: -8, -106, -10), R cerebellum (peak voxel: 32, -82, -24), L ventral precuneus (peak voxel: -6, -70, 16), and L precentral gyrus (peak voxel: -38, -4, 58). When the behavioral measure reported here was computed using only non-recalled items (Figure 4.11B), the effects are more localized in a more posterior and ventral direction, with one large cluster in bilateral occipital cortex (peak voxel: 4, -86, 22), and another cluster (peak voxel: -52, -76, -6) extending from L lateral occipital cortex into L posterior lateral temporal cortex. Note that analogous whole-brain analyses using data from the cue period showed no significant clusters.

Although no effects with this behavioral measure emerged in young adults, we also wanted to directly compare the strength of effects for young adults versus older adults to determine whether they are reliably stronger in older adults. However, when all items are included in computing the process estimates, the only significant cluster to emerge is a small cluster in L inferior medial occipital cortex (peak voxel: -14, -98, -14). In the analysis run with process estimates computed using only non-recalled items, there is a somewhat larger cluster (peak voxel: 8, -86, 30) in bilateral occipital showing a reliable difference in this effect. These findings mean that there is not a reliable age difference in any of the more theoretically interesting regions in frontal and parietal cortex that show up for older adults but not for young adults. Still, while that limits the conclusions that we can draw about age differences, we can still draw conclusions from the findings that are present within the older adult sample.

Finally, we examine whether any of the ROIs that were discussed above show a reliable correlation with this R/F difference measure. In older adults, when the process estimates are computed using all items, all 3 ROIs related to semantic processing show a significant correlation with the difference measure: the Neurosynth semantic ROI, $r = .61$, $p = .005$, the L BA 45/47 ROI, $r = .49$, $p = .032$, and the L BA 44/6 ROI, $r = .59$, $p = .008$. None of these correlations are significant when only non-recalled items are used to compute process estimates, all $|r| < .26$, $p < .307$, nor were correlations in any of these ROIs significant during the cue period, $|r| < .28$, $p > .243$. Effects in these 3 ROIs were not significant in young adults during the word period or the cue period, using all items or nonrecalled items, all $|r| < .25$, $p > .320$. However, the significant effects with older adults also did not differ significantly from the analogous effects in young adults.

For older adults, we do also see effects of the R/F difference measure in reward-sensitive brain regions. During the cue period, there is a significant correlation in the NAcc ROI, $r = .60$, $p = 006$, and a marginal correlation in the Neurosynth reward ROI, $r = .41$, $p =$

.082. During the word period, there is a significant correlation in the Neurosynth reward ROI, $r = .51$, $p = .027$, and a marginal effect in the NAcc ROI, $r = .39$, $p = .095$. Similar to the effects described above, these effects are not significant in older adults when only non-recalled items are used to compute process estimates, all $|r| < .21$, $p > .419$. In addition, none of these effects are significant in young adults regardless of whether recalled items are included in the computations, all $|r| < .29$, $p > .299$, but the significant effects described above for older adults are also not significantly different from the analogous effects in young adults.

Finally, we examine whether correlations with the R/F difference are present in the ROIs described above as having shown negative subsequent memory effects in prior studies. For older adults during the word period, looking at the five ROIs from the Mattson et al. (2014) study, we find a significant correlation in the L precuneus ROI, $r = .60$, $p = .006$, and a marginal correlation in the L TPJ ROI, $r = .41$, $p = .081$. Analogous correlations with other ROIs were not significant: dorsal R precuneus, $r = .35$, $p = .137$, ventral R precuneus, $r = -.02$, $p = .93$, and midcingulate, $r = -.23$, $p = 338$. Again, no correlations during the cue period were significant, all $|r| < .24$, $p > .325$. In addition, there were no significant correlations in these ROIs when non-recalled items were used to compute the behavioral measure; outside of a single marginal effect in the negative direction for L TPJ during the cue period, $r = -.44$, $p = .08$, all other $|r| < .31$, $p > .228$. In young adults, there was a marginal effect in the L precuneus ROI during the cue period for the analysis using all items, $r = .46$, $p = .053$, but no other effects during the cue period or word period, using all items or only non-recalled items, were significant, all $|r| < .29$, $p > .245$.

When examining the ROIs generated from the Kim (2011) meta-analysis, the only significant correlation with the R/F difference measure was a negative correlation in R precuneus during the word period in older adults, when the behavioral measure is computed using non-recalled items, $r = -.49$, $p = .045$. In this region, it seems that the difference in activation as a function of value seemed to correlate negatively with value effects on recollection but positively with effects of value on familiarity, a reversal of the pattern found in the other regions described above. No other effects in this set of three ROIs are significant across cue period or word period, using either all items or non-recalled items to compute the behavioral measure, in young or older adults, all $|r| < .36$, $p > .186$. While the R precuneus effect that is significant does not survive correction for multiple comparisons, it is still notable in suggesting that the opposing effects for recollection vs. familiarity in older adults may hold true even in areas for which increased activation leads to less recollection and greater familiarity, a reversal of the pattern that we see in the other regions described above.

Discussion

The behavioral results suggest that in older adults, both recollection and familiarity are strengthened for high-value items. The finding that value leads to a significant increase in familiarity as well as recollection is distinct from what we saw in Experiment 1A in young adults, in which value led to increased recollection, even for non-recalled items, but effects on familiarity were inconclusive. In older adults, a significant portion of the improvement in memory for high-value items, at least on a delayed recognition test, seems to be driven by increased familiarity. We also find that in older adults, the effects of value on recollection are only present when the computation of process estimates includes items that were freely recalled, while familiarity is stronger for high-value items regardless of whether process estimates include freely recalled items as well as non-recalled items, or only non-recalled items.

Thus, it is possible that in older adults, enhancements in recollection by value are being driven partly or entirely by recollection of the experience of recalling items on the recall test, rather than recollection of the original study experience. Still, if we were to conclude that the effect of value on recollection in older adults is entirely artifactual, we would have to assume that the substantial effect of value on free recall performance (see Chapter 3) is driven entirely by familiarity, but then the experience of the free recall tests themselves are able to be recollected. This seems an unlikely hypothesis given prior work establishing that free recall generally depends primarily on recollection (Yonelinas, 2002). One alternate possibility is that nearly all of the items for which value-directed encoding strategies strengthened episodic encoding enough to produce recollection were able to be freely recalled, leaving very few residual recollected but non-recalled items for the recognition test. This explanation would suggest that recalled items that are then recollected on the recognition test probably would have been recollected even if not for the experience on the free recall test, which would also mean that the process estimates computed using all items are an appropriate measure for further analyses.

A different alternative explanation is that in older adults, many of the items that were initially capable of being recollected, but for which free recall failed, lost their episodic memory trace during the 30-60 minute retention interval (cf., Knowlton & Squire, 1995; Dudukovic & Knowlton, 2006). By this interpretation, it is possible that, even if value effects on the initial free recall test were being driven by enhanced recollection, those recollection effects may have dissipated by the time of the recognition test. In young adults, episodic information might remain for a longer duration, which is why young adults would be able to show value effects on recollection of non-recalled items even after a substantial delay. By this explanation, it is possible that value effects on recollection in the recognition test are an artifact of the strengthening of episodic memory in the free recall test, even if value effects on the initial free recall test were largely driven by episodic recollection of the original study event, and thus the process estimates computed using all items would not be an appropriate measure of memory under the test conditions used in this experiment. Further work would be necessary to distinguish between these explanations.

In relating the fMRI data to effects of value on recollection and familiarity during the recognition test, one notable effect is the correlation found in both young and older adults between brain activity in semantic processing regions and effects of value on recollection. However, in both age groups, correlations between the degree of increased activity in semantic processing regions and the corresponding degree of increased recollection found across all items was significantly reduced and no longer reliable when the recollection estimates were computed with only non-recalled items. Thus, increased activity in semantic processing regions likely either created increased recollection for freely recalled items that was maintained through the recognition test, or it led to increased performance on the free recall test, which led to greater recollection on the later test. By either of these explanations, the effects in semantic processing regions that we report in this section can be considered not much more than a recapitulation of the results shown in Chapters 2 and 3.

The negative subsequent memory effects seem more interesting, however, particularly because age differences in these effects seem to correspond particularly well with age differences in the behavioral data. To recap, we found negative subsequent memory effects that correspond with recollection in young adults, and the strength of those correlations was not significantly weakened when only non-recalled items were used to compute process estimates. Behaviorally, young adults show a significant effect of value on recollection even when recalled items are excluded, even though the correlations with value-related differences in semantic processing regions of the brain go away under those conditions. Thus, it could be that the ability to more strongly deactivate default-mode network regions during encoding of high-value items helps young adults create memories that can be recognized with high confidence at a substantial delay even when initial recall has failed. Older adults do not seem to show a value-related difference in the ability to recognize non-recalled items with high confidence after failing to recall items on the initial recall test, and correspondingly, they do not tend to show any negative correlations between value-related differences in recollection and the degree to which brain regions that tend to show reverse subsequent memory effects are more deactivated during encoding of high-value items. The negative brain-behavior correlations shown with recollection in young adults also show reliable age differences between young and older adults (see Figure 4.8), confirming that their presence is significantly stronger in young adults.

Older adults do, however, show negative brain-behavior correlations that correspond to value-related differences in familiarity rather than recollection. Specifically, weaker value-related differences in brain activity during encoding, particularly in medial posterior cortical regions, seem to correlate with stronger effects of value on subsequent familiarity. Given that older adults, unlike younger adults, show significant value-related increases in familiarity strength for high-value items on the recognition test, it may be that negative brain-behavior correlations underlie this behavioral effect as well. The negative effects observed here are in the vicinity of negative subsequent memory effects shown in other studies (e.g., Kim, 2011), as well as in the vicinity of the regions in which we found negative subsequent memory effects on recollection in young adults in Experiment 1A. However, the ROI analysis using the peaks from the Kim (2011) meta-analysis showed that the negative subsequent memory analysis on familiarity in the present study do not quite overlap with where negative subsequent memory effects are typically found.

In contrast, the negative subsequent memory effects that we observe in older adults seem to correspond to the regions in which Mattson et al. (2014) found subsequent memory effects on familiarity-based (item) memory in young adults, but *not* in older adults. They found that young adults tend to disengage brain regions that distract from successful encoding, and the regions that are relevant here seem to be particularly likely to distract from the type of encoding that leads to item recognition independent of accurate source memory. In their study, older adults do not show a comparable pattern of disengagement. Thus, it seems counterintuitive that, in our study, we would see the reverse pattern of age effects, as older adults show negative brain-behavior correlations in these regions but young adults do not. Still, even if older adults do not spontaneously disengage those regions across an entire memory task, it is possible that older adults may still vary the degree to which they engage or disengage these areas between encoding high-value vs. low-value items. Such a distinction would be comparable to the distinction between the finding that older adults are less likely than are young adults to spontaneously engage deep encoding processes during an intentional encoding task, as indicated by the level of brain activity in left VLPFC (Logan et al., 2002), but yet older adults are still able to modulate activity in left VLPFC as a function of value in the value-directed remembering task (Chapter 3). It may be the case that older adults can also modulate, as a function of value, the relative engagement or disengagement of parietal and occipital regions that distract from the type of encoding that leads to familiarity, either via an automatic attentional orienting mechanism, or via strategic processes.

It is still not entirely clear why the negative brain behavior correlations would be in a slightly different location in older adults as compared to young adults, although one possible explanation is merely that the brain regions that perform particular functions shift somewhat in older adults to compensate for differential age-related degradation in different brain regions (see Chapter 3, as well as Rajah & D'Esposito, 2005, for similar explanations). Another question is why negative brain-behavior correlations are found to affect familiarity in older adults but recollection in young adults. A simple explanation there could be that memory, and particularly the episodic detail that leads to recollection, decays faster for older adults than for young adults. Thus, it is possible that a similar deactivation of unproductive internally-directed cognition is signified by the negative brain-behavior correlations in both age groups. The memory boost created by this mechanism may not be enough to consistently allow for free recall, but in young adults, there is still a strong enough memory trace to allow for episodic recollection on a recognition test. In older adults, however, as discussed above in the context of explaining age differences in the behavioral data, the episodic information may fade by the time of recognition test is given, and the memory boost that remains for those items would be in the form of enhanced familiarity.

However, another notable result from these analyses, which does not seem to be accounted for by the above explanation, is that greater value-related modulation of activity in some of the same brain regions is associated with both greater recollection-driven memory but reduced familiarity-driven memory. Such effects are apparent in the left precuneus cluster associated with negative subsequent memory effects in the Mattson et al. (2014) study, but also in some of the same semantic processing areas in which increased activation at encoding benefits performance on the free recall test (see Chapter 3), and in reward-processing regions as well. A speculative explanation for these results is that effects of value on familiarity in older adults reflect a secondary, low-effort means by which value enhances memory. It is clear that older adults are able to be selective in their use of elaborative encoding mechanisms, and these mechanisms clearly seem to underlie successful selectivity in older adults to a significant degree, as is apparent based on the results reported in Chapter 3. However, it may be too taxing for older adults to engage these processes consistently, and thus, value may also modulate encoding-related activity via less effortful mechanisms some of the time.

There may, in other words, be a tradeoff between increased engagement of effortful processes, such as elaborative encoding, that are more likely to lead to episodic recollection and successful free recall, versus low-effort processes that allow a more basic memory trace to be established. One reason for such a tradeoff is that, for instance, internally-directed cognition may help with generating connections between items, but if not carefully controlled, it could also lead to distraction from the task at hand. Young adults may have an easier time keeping such processes under control, and thus they would have less need to deactivate mental processes that can be beneficial, even if they do begin to get fatigued in the scanner. They may be able to simultaneously show stronger deactivation of regions that distract from successful encoding, a lower-effort process that can lead to some additional memory enhancement for high-value items, at the same time as they attempt to engage processes that benefit deep encoding, and even if the latter processes fail, the former can still help them to some degree. When older adults get fatigued, however, because they may have a harder time controlling the processes involved in elaborative generation and encoding, and they may need to disengage areas involved in such processing and focus more on low-effort mechanisms, as they could end up performing worse if they try to engage both mechanisms in the way that young adults do. In older adults, the low-effort mechanisms associated with these negative brain-behavior correlations may lead to enhancements in familiarity rather than recollection, and are thus less likely to improve performance on the free recall test than elaborative encoding. Still, older adults may assume that it is better to try to get some advantage for high-value words via low-effort strategies than to get distracted by trying and failing to control elaborative encoding mechanisms, or to ignore value completely.

Experiment 2

The next five experiments represent an attempt to address, via behavioral methods in young adults, questions that were left unanswered by Experiment 1. One question is whether the effects of value that we found via ROC curves replicate using other methods to dissociate recollection from familiarity. Particularly given the relatively small number of old non-remembered trials present in some individuals, even when those individuals who had an extremely low number of trials were excluded, and also given evidence that different methods of separating processes can lead to differing results (e.g., Prull et al., 2006), it seemed that any results generated by the ROC analysis should be confirmed via another method. Another goal was to have a larger sample size in order to better clarify effects of value during encoding on familiarity, given that Experiment 1A was not able to say anything conclusive about these effects. To address these goals, we made some minor modifications to the encoding paradigm used in other parts of this work, and used an R/K procedure as part of the recognition test following encoding.

Methods

Participants. 43 participants were recruited from the UCLA undergraduate psychology subject pool, which includes undergraduate students from introductory psychology, linguistics courses, as well as more advanced psychology courses. One additional participant was run but was replaced due to an experimenter error.

Materials. The study items presented in the value-directed remembering task, and the lure words used in the recognition test, were largely identical to those used in the fMRI study. However, because we included 144 old items instead of 120 old items on the recognition test (excluding only the first list, rather than the first two lists), we also added another 24 lure items to the recognition test, in order to equate the number of lure items with the number of old items. These items were selected based on the same criteria as other words used in this set of studies.

Procedure. The basic procedure is similar to that originally described in Chapter 2. After reading through the instructions on-screen, participants saw 6 practice items intended to familiarize them with the encoding paradigm. Then, after the experimenter answered any questions that arose, seven complete study lists were presented. As in the fMRI paradigm, each list included 24 items, half of which were low-value (worth 1, 2, or 3 points), and half of which were high-value (worth 10, 11, or 12 points), with the assignment of words to value group counterbalanced across subjects.

However, the paradigm was modified to eliminate some of the design features that had originally been introduced to make the paradigm compatible with fMRI. Each trial in the encoding paradigm began with an initial value cue, presented for 1 s, followed by a fixation period lasting 0.5 s. The word was then shown for 2.5 s, followed by a 2 s blank screen before the next item was presented. The vowel-consonant task was also eliminated, as were all extended rest periods at the beginning and end of each list, as these features were only needed for fMRI analysis. After each list of 24 items was presented, participants were instructed to freely recall as many items as possible from the list that they just saw, and were given 60 seconds to do so verbally. The experimenter was in the room with the subject during the entirety of the encoding portion of the paradigm, and provided immediate feedback as to how many points they earned.

Following the encoding task, participants played the video game Snood for approximately 5 minutes. Then, they began the recognition test, receiving careful instructions about the definition of Remember and Know. Instructions were adapted from those used by Rajaram (1993). Specific instructions were as follows:

> “You should make a Remember judgment if you can consciously recollect what you experienced when you studied the word earlier. This may include aspects of the physical appearance of the item, of something that happened in the room, or of what you were thinking or doing at the time. You should make a Know judgment if you recognize the item as being one that you studied, but you cannot consciously recollect what you experienced while studying it. In other words, choose "Know" when you are fairly certain that

> you recognize the item, but it fails to evoke any specific conscious recollection of your experience learning that word.
> Consider the following examples. If I asked you to remember eating breakfast this morning, you'd likely be able to recollect where you were, what you ate, and what you were thinking about. You would thus give a "Remember" response. However, in another situation, you may see someone on campus and know that you've met that person before, but you have no idea where and can't remember anything else about him or her. In this situation, you would give a "Know" response."

After reading these instructions, participants were instructed to describe to the experimenter the difference between an R and a K judgment. This was an added check to ensure that they had paid attention to the instructions, and an opportunity for the experimenter to correct any misunderstandings.

Another important design feature was the use of two-stage remember/know judgments with no "guess" option. Participants were first instructed to judge whether an item was "old" or "new", and were told that they should only choose "old" if they are "fairly confident" that they saw the word, but should choose "new" if they either did not remember seeing the word, or if they were unsure. Then, only once they had chosen the "old" option did they make a judgment as to whether the item best matched an R or a K response. This procedure has been shown to reduce the use of "Know" as a low-confidence response (Eldridge, Sarfatti, & Knowlton, 2002), which is important because a key assumption in the Remember/Know paradigm is that the two judgments should be relatively equated in terms of confidence, but just vary in terms of the quality of the memories.

Participants were allowed as much time as they wanted to respond to each item. Words appeared one at a time on the screen, and the word remained on-screen until a key was pressed to indicate "old" or "new". If "old" was chosen for a given word, then the word disappeared from the screen, and they had to judge the item that they just saw as being a "Remember" or a "Know" item. This procedure repeated for all 288 items on the recognition test. After the recognition test was complete, participants completed a post-study questionnaire, which asked them to write down the basis on which they made Remember and Know judgments, as an additional check that we could use to confirm that they understood the procedure. This questionnaire also asked about what they did differently during the encoding procedure for high-value vs. low-value items, which we used to classify people based on how strongly they described their encoding processes as being affected by the value of the word being studied. This classification is discussed further below.

Results

Free Recall. We begin by analyzing performance on the free recall test. Note that list 1 is generally treated as a practice list, as items from this list were not included in the recognition test for this or any of the following experiments. Thus, only data from lists 2-7 are included in computing free recall scores here. Averaging across these 6 lists, the proportion of high-value items recalled ($M = .523$, $SD = .162$) was significantly higher than the proportion of low-value items recalled ($M = .270$, $SD = .184$), $t(42) = 6.97$, $p < .001$. We also examined selectivity index using the formula presented in Chapter 2. Selectivity index was computed separately for each list, and an unweighted average was computed across lists 2-7. (Although a weighted average was used in Chapter 3, and wherever selectivity was referenced in Experiment 1A and 1B of this chapter, a simpler unweighted average seemed more appropriate for experiments that only test young adults. In any case, the two measures tend to be almost identical, particularly for young adults.) Overall, mean selectivity (*M* = .334, *SD* = .304) was significantly greater than zero, $t(42) = 7.21$, $p < .001$. These results confirm that value had a strong effect on behavior in this version of the value-directed remembering paradigm.

Remember/Know results. Because there is still some controversy regarding whether the Yonelinas & Jacoby (1995) correction for independence is in fact the most valid way to analyze data from the Remember/Know paradigm, data are presented here both with and without the correction applied. In addition, the issue noted in Experiment 1, whereby memory performance on the recognition test may be enhanced by memories of the experience of recalling a given item on the free recall test, rather than reflecting purely memory of the initial study event, is still a concern in this and in the other experiments that follow. Thus, for each analysis, data are presented first for all items, and again looking only at non-recalled items.

In this experiment, when all items are considered, there is a significant effect of value on the raw proportion of items given R responses, $t(42) = 6.40$, $p < .001$, but no effect of value on the raw proportion of items given K responses, $t(42) < 1$. A 2 x 2 (process x value) repeated-measures ANOVA shows that there is a significant interaction between these two factors, $F(1, 42) = 24.45$, $MSE = .021$, $p < .001$, $\eta_p^2 = .37$ (Figure 4.12A). When only non-recalled items are included in the analysis, we see a similar pattern of effects, as there is a significant effect of value on R responses, $t(42) = 6.03$, $p < .001$, but no effect of value on K responses, $t(42) = 1.29$, $p = 203$. The interaction is again significant here, $F(1, 42) = 8.28$, $MSE = .013$, $p = .006$, $\eta_p^2 = .17$. Thus, when using raw K responses as our measure of familiarity, it would appear that value leads to an increased rate of R responses but no change in the rate of K responses.

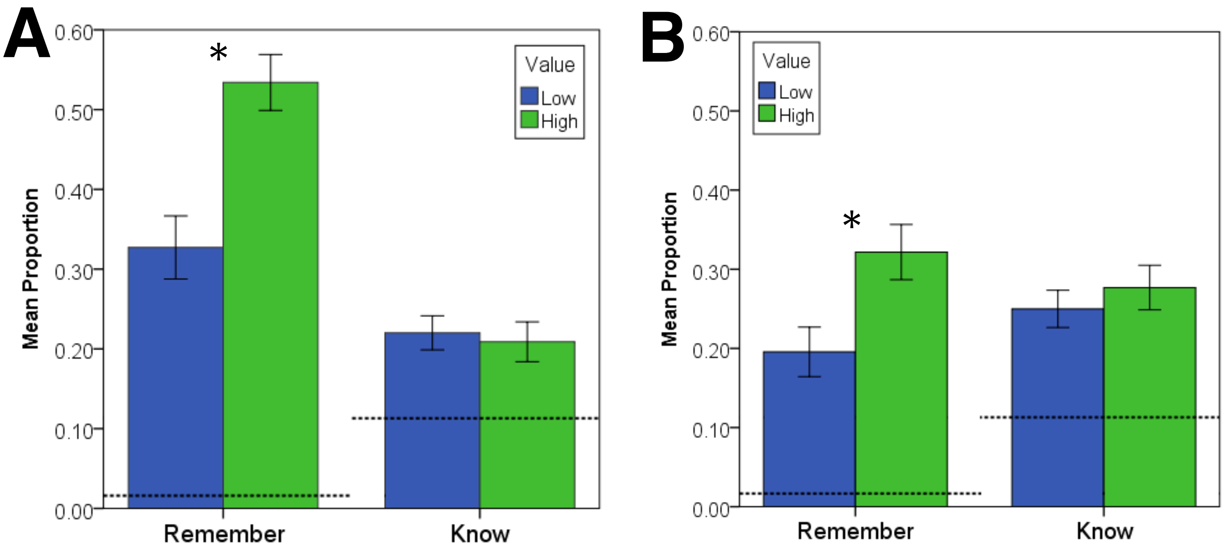

Figure 4.12. Raw (uncorrected) proportion of items given Remember and Know responses, computed using (A) All items, and using (B) Non-recalled items, in Experiment 2. Dashed lines represent false alarm rates for Remember and Know items, respectively. Error bars represent +/- 1 SE.

The pattern of effects is different if we assume that R and K are independent rather than mutually exclusive, applying the Yonelinas and Jacoby (1995) correction. For R responses, this correction does not affect the relationship between value and response proportions, as it only corrects for false alarms, which are equivalent for both high- and low-value items. Thus, there is no need to re-compute the statistics for this measure. When using the correction factor to generate familiarity estimates from the proportion of K responses, however, the effect of the correction does vary substantially between conditions. When applying the correction to the response proportions, but including all items in the analysis, we find that familiarity is greater for high-value items than for low-value items, $t(42) = 3.38$, $p = .002$. In this case, the process x value interaction is still significant, $F(1, 42) = 10.04$, $MSE = .014$, $p = .002$, $\eta_p^2 = .19$, suggesting that the effect of value on recollection is larger than the corresponding effect on familiarity, even when both are significant (Figure 4.13A). When only non-recalled items are included in the analysis,

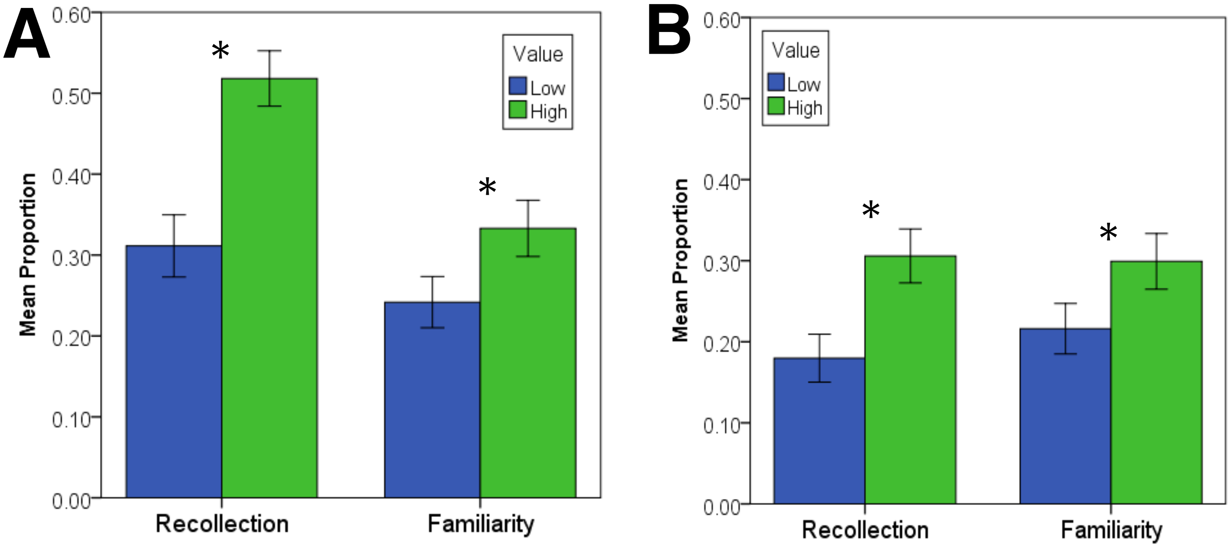

Figure 4.13. Recollection and Familiarity estimates, after applying the correction for independence of the two processes, and also correcting for false alarms, computed using (A) All items, and using (B) Non-recalled items, in Experiment 2.

the effect of value on familiarity remains significant, $t(42) = 3.46$, $p = .001$. In this case, the process x value interaction is not significant, $F(1, 42) = 1.89$, $MSE = .010$, $p = .176$, $\eta_p^2 = .043$ (Figure 4.13B). These results clearly show that when the correction for independence is applied, high-value items show both greater recollection and greater familiarity.

Effects of individual differences in strategy use. A final key question in running this experiment was to begin to examine how the strategically-driven effects of value, in terms of explicit changes in the application of effective encoding strategies as a function of value, contrast with automatic effects of value, which may be driven by the enhanced dopaminergic response to rewards. One way to get at this distinction is to separate individual participants on the basis of how strongly they report applying different strategies for high-value or low-value items. To do so, the first author made a subjective assessment of responses on the post-study questionnaires, and assigned each participant to one of three categories. The first group, low strategy use (n = 13), generally claimed to be insensitive to value. People in the second group, moderate strategy use (n = 14), generally claimed to have "tried harder," or something similar, for high-value items, but still seemed to apply some effort to low-value items as well. The third group, strong strategy use (n = 15), claimed to either ignore low-value items completely (n = 6), or had a specific encoding strategy that they only applied to the high-value items (n = 9). While we had initially hoped to divide these two subcategories of the strong strategy group into separate groups, they were ultimately combined into a single group in order to have sufficient power for analyses. Finally, one participant did not provide an adequate response to assess strategy use, so that participant was excluded from the analyses that follow.

To confirm that the assignment of subjects to groups was sensible, we examine how they differ in terms of free recall performance. A 2 x 3 (value x strategy group) mixed ANOVA, with repeated measures on the first factor, confirms that there is an interaction between item value and strategy group, *F* (2, 39) = 15.34, *MSE* = .017, *p* < .001, η_p^2 = .44 (Figure 4.14). We used paired-samples t-tests to probe the interaction, comparing the number of high-value vs. number of low-value items recalled within each group. In the low strategy group, there is not a reliable effect of value on recall performance, *t*(12) = 1.07, *p* = .305, while reliable effects of value on recall are present in the moderate

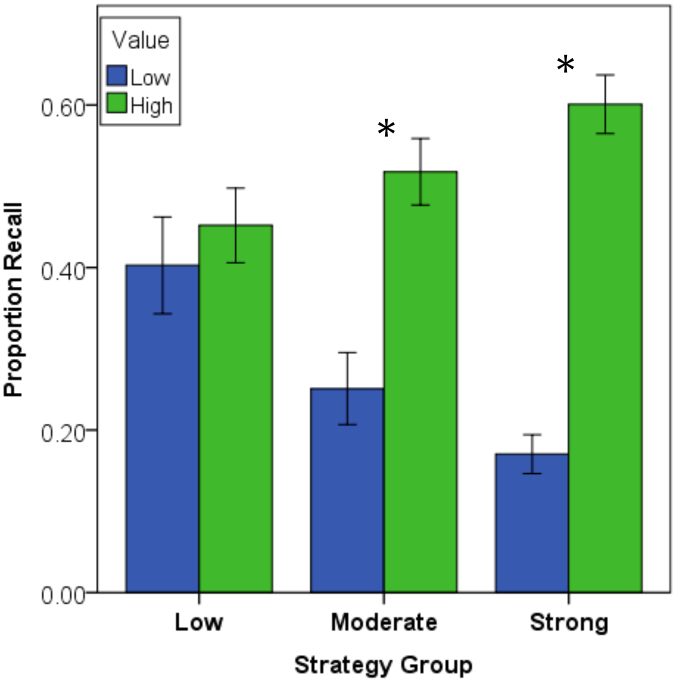

Figure 4.14. Effects of value on free recall performance on lists 2-7, divided by the strategy group assigned on the basis of post-study questionnaires, in Experiment 2. Error bars represent +/- 1 SE.

group, $t(13) = 4.70$, $p < .001$, as well as in the strong group, $t(14) = 10.17$, $p < .001$.

Using a one-way ANOVA, we see that there is also a reliable effect of strategy group on selectivity index, $F(2, 39) = 13.86$, $MSE = .057$, $p < .001$, $\eta_p^2 = .42$. Post-hoc Tukey tests show that the Low group differs from the Moderate group, $p = .011$, and from the Strong group, $p < .001$, while the difference between the Moderate and the Strong group is marginal, $p = .087$. Finally, using one-sample t-tests, we find that selectivity index in the Low group ($M = .08$, $SD = .24$) is not reliably different from zero, $t(12) = 1.17$, $p = .264$. Selectivity index in the Moderate group ($M = .36$, $SD = .28$) is reliably above zero, $t(13) = 4.88$, $p < .001$, as is selectivity in the Strong group ($M = .55$, $SD = .19$), $t(14) = 11.40$, $p < .001$. Thus, it seems that there is not a reliable effect of value on recall in the Low strategy use group. Value does reliably affect recall in both the Moderate and the Strong strategy use groups, although the trend is for value effects to be more robust in the Strong group.

We then examine how value affects performance on the R/K recognition test for the different strategy groups. For this analysis, we only look at corrected process estimates. One reason is that, as discussed in the Introduction, prior literature has supported the idea that the corrected R/K procedure yields more valid results than uncorrected R/K proportions, particularly if the conclusions that could be drawn with the two different methods differ, as they do here. In addition, based on prior literature (e.g., Gardiner, 1988), we would expect no difference in raw K responses if people were selectively applying deep encoding strategies to high-value items, and we would also expect no difference in raw K responses if value were having an effect via more automatic mechanisms (cf., Wittmann et al., 2011). However, corrected familiarity estimates should be able to distinguish between these mechanisms, as depth of processing manipulations at encoding do lead to an increase in familiarity estimates when the processes are assumed to be independent (cf., Yonelinas, 2002), but automatic mechanisms are less likely to do so, as discussed in the introduction.

We therefore examine how value affects process estimates separately for each strategy use group, both when considering all items (Figure 4.15A), and when considering only non-recalled items (Figure 4.15B). In the Low strategy use group, looking at all items, the effect of value on recollection is marginal, $t(12) = 2.11$, $p = .056$, while there seems to be no effect of value on familiarity, $t(12) < 1$. When looking only at non-recalled items, there is a significant effect of value on recollection, $t(12) = 3.51$, $p = .004$, but still no effect of value on familiarity, $t(12) < 1$. The process x value interaction is significant both when considering all items, $F(1, 12) = 5.06$, $MSE = .009$, $p = .044$, $\eta_p^2 = .30$, and when considering only non-recalled items, $F(1, 12) = 5.90$, $MSE = .008$, $p = .032$, $\eta_p^2 = .33$.

In the Moderate strategy group, when considering all items, high-value items show both better recollection, $t(13) = 3.89$, $p = .002$, and better familiarity, $t(13) = 2.83$, $p = .014$. When considering non-recalled items, we again see value-related increases both for recollection, $t(13) = 3.30$, $p = .006$, and for familiarity, $t(13) = 2.80$, $p = .015$. In this group, there is a weak, non-significant trend towards a process x value interaction for all items, $F(1, 13) = 2.95$, $MSE = .007$, $p = .109$, $\eta_p^2 = .185$, such that value tends to have a somewhat stronger effect on recollection than on familiarity; this trend goes away entirely when looking only at non-recalled items, however, $F(1, 13) < 1$. The effects are largely similar in the Strong strategy group. When all items are considered, effects of value are reliable for both recollection, $t(14) = 6.26$, $p < .001$, and for familiarity, $t(14) = 3.53$, $p = .003$. When only non-recalled items are considered, effects of value are again reliable for both recollection, $t(14) = 4.23$, $p = .001$, and for familiarity, $t(14) = 3.67$, $p = .003$. In this group,

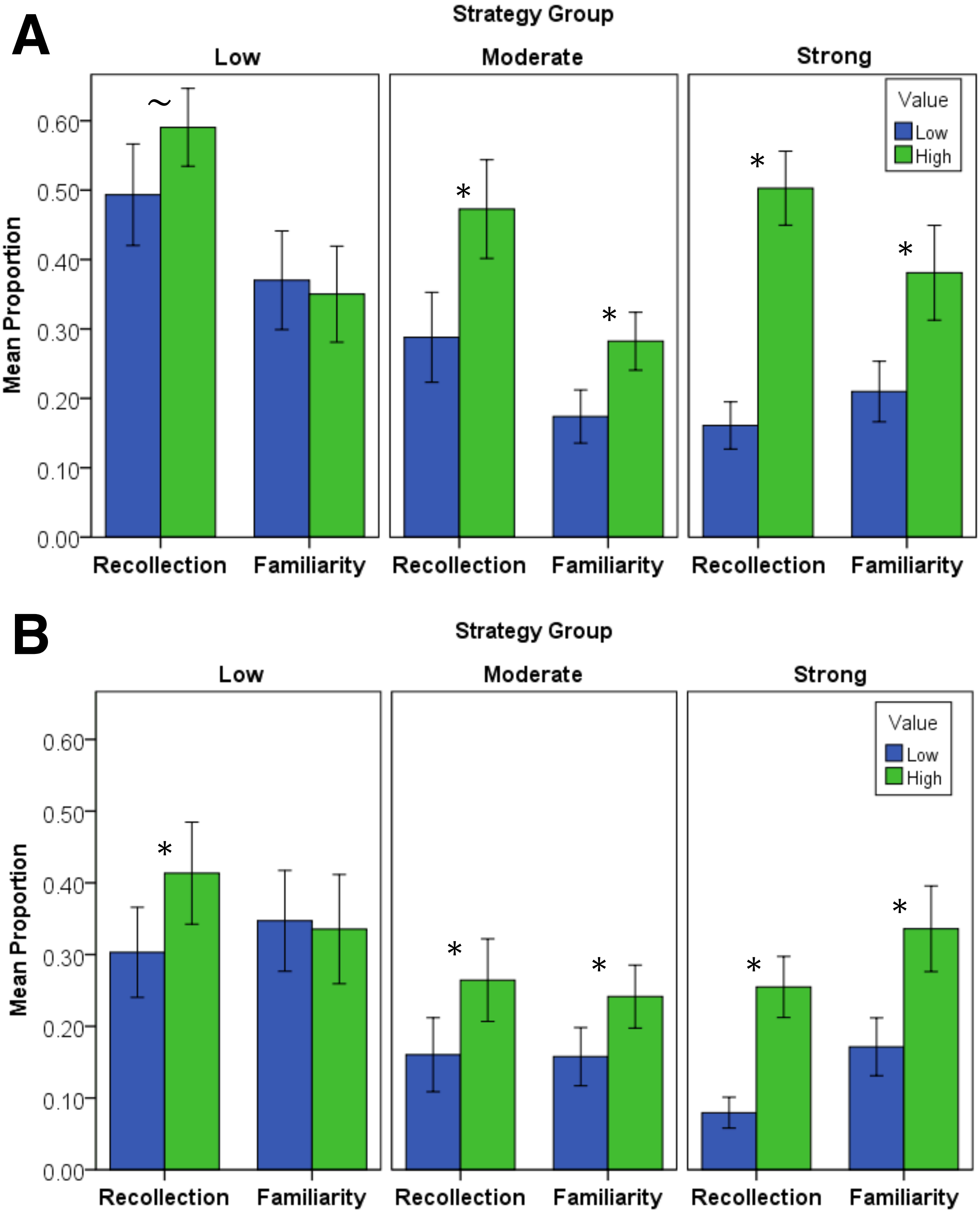

Figure 4.15. Effects of value on corrected recollection and familiarity estimates, split based on assignment of participants to strategy groups based on post-study questionnaires, considering (A) all items, and (B) non-recalled items, in Experiment 2. Error bars represent +/- 1 SE.

we also find that when all items are considered, there is a marginally-significant trend towards an interaction between value and process, $F(1, 14) = 4.18$, $MSE = .026$, $p = .06$, $\eta_p^2 = .23$, such that value has a stronger effect on recollection. When only non-recalled items are considered, however, the interaction is clearly not significant, $F(1, 14) < 1$.

Another way to examine how value effects on the two processes differ as a function of explicit strategy use is to look separately at interactions between value and strategy group for recollection, and for familiarity. When looking at all items, a 2 x 3 (value x strategy group) mixed ANOVA on recollection finds an interaction between value and strategy group, $F(2, 39) = 6.21$, $MSE = .018$, $p = .005$, $\eta_p^2 = .241$. A similar ANOVA looking at familiarity also finds an interaction between value and strategy group, $F(2, 39) = 4.83$, $MSE = .014$, $p = .013$, $\eta_p^2 = .20$. When looking only at non-recalled items, the value x strategy group interaction on recollection is not significant, $F(2, 39) = 1.27$, $MSE = .009$, $p = .293$, $\eta_p^2 = .06$, but the analogous interaction effect on familiarity is still significant, $F(2, 39) = 5.11$, $MSE = .011$, $p = .011$, $\eta_p^2 = .21$. It seems likely that the effect of strategy group on recollection is being driven by items that are recalled on the free recall test, but the interaction effect for familiarity is present both for all items and for non-recalled items.

Discussion

In this experiment, we replicated the finding from Experiment 1A showing that value leads to consistently increased recollection in young adults, even for items that were not recalled on the free recall test. Interestingly, it seems that this effect holds true even when participants claimed to treat high-value and low-value items equally, despite the fact that those individuals in fact did not show an advantage for high-value items on the free recall test. The fact that similar effects of value on recollection are observed in a subset of subjects who claimed to not do anything differently for high-value items suggests that these effects are automatic, rather than strategically mediated.

The data from this experiment, at least at first glance, still leave some ambiguity as to whether value does in fact affect familiarity. There are no value-related differences in the uncorrected rate of K responses, but there is a reliable value-related increase in familiarity estimates obtained when the K response rate is corrected to follow an independent process assumption (Yonelinas & Jacoby, 1995). Experiments 4-6 in this chapter will attempt to clarify this issue using a different method that does not require assumptions to be made about the nature of the relationship between familiarity and recollection. However, as discussed in the Introduction, the available evidence (e.g., Sheridan & Reingold, 2012) does seem to suggest that the independence assumption yields objectively more valid results than does the exclusivity assumption inherent in the use of raw K responses. Thus, if one had to choose, it seems that the results obtained using the corrected familiarity estimates are more likely to be accurate.

These results are in line with previous findings (Yonelinas, 2002) showing that, when recollection and familiarity are assumed to be independent processes, encoding manipulations such as deep levels of processing and generation strategies lead to increased familiarity as well as increased recollection. That is the pattern that we find in our corrected process estimates, both when averaging across the entire sample, and when looking only at individuals who claim to be making an effort to enhance encoding for high-value items. In contrast, individuals who claim to not be making an effort to improve encoding for high-value items do not show a benefit for high-value items in familiarity. Together with prior literature suggesting improved recollection but no enhancement in familiarity when value enhances memory via automatic, dopamine-driven mechanisms (e.g., Shigemune et al., 2014; Wittmann et al., 2005, 2011), the combined findings further support the idea that effects of value on subsequent recollection of nonrecalled items, in the absence of value effects on recall or on familiarity, are being driven by automatic mechanisms.

Experiment 3

A question that remains outstanding at this point is what effect the inclusion of free recall tests and feedback have on the mechanism by which value typically enhances memory in the value-directed remembering paradigm. The opportunity for participants to gain experience with how successful they are at utilizing value cues to enhance memory encourages the use of metacognitive monitoring and control, a key difference between this paradigm and other paradigms that have been used to examine more automatic effects of value on memory (cf., Adcock et al., 2006). In Experiment 3, we used a paradigm identical to that used in Experiment 1, except that we removed the free recall tests and associated feedback. Here, the only test is an R/K recognition test similar to that used in Experiment 2. We expected that this manipulation would weaken any effects of value on memory that are related to the selective application of strategies, allowing us to gain a better understanding of what role metacognitive strategies play in the mechanisms by which memory is improved for high-value items in the value-directed remembering paradigm.

Method

Participants. We tested 46 individuals from the UCLA Psychology department undergraduate student subject pool in this study. 12 additional participants in one of the two counterbalancing conditions were run but were replaced, due to an error in the program for that condition.

Materials and Procedure. The materials and procedure in this study were identical to those used in Experiment 2, with the exception of the fact that no free recall tests were administered during the encoding task. Words were still presented in distinct lists of 24 items; however, at the end of each list, instead of having a recall test, participants were merely told that they had reached the end of the current list, and they could press a key to continue on to the next list when they were ready. In addition, during the initial instructions for this experiment, participants were told that they would be given a yes/no recognition test later on the words that they were learning. They were also told that on the later recognition test, they would receive the point value presented at encoding if they recognized the word, while they would lose 1 point for any incorrect "yes" responses during the recognition test. No feedback regarding scores was given during the recognition test, however. Note that in the preceding studies, the recognition test was never mentioned prior to the beginning of that test. However, given that we did still want this task to be an intentional encoding task, it seemed that some explanation would be necessary as to when and how the values would become relevant.

Results

Remember/Know results. In this version of the paradigm, no recall test was administered, so the available data are somewhat simpler. Specifically, only recognition data are available, and there is no need to distinguish between recalled and non-recalled items. We find that there is an effect of value on uncorrected Remember responses, t(45) = 3.50, p = .001, but there is no effect of value on uncorrected Know responses, t(45) = 1.59, p

= .118. Indeed, if anything, the apparent trend is for there to be more K responses for low-value items than for high-value items. A 2 x 2 (process x value) within-subjects ANOVA finds that the interaction between these factors is significant, $F(1, 45) = 12.96$, $MSE = .004$, $p = .001$, $\eta_p^2 = .22$ (Figure 4.16A). When applying the Yonelinas and Jacoby (1995) correction to assume independent processes, there is still not a reliable effect of value on familiarity, $t(45) < 1$, and the process x value interaction remains significant, $F(1, 45) = 9.16$, $MSE = .003$, $p = .004$, $\eta_p^2 = .17$ (Figure 4.16B). Thus, the results differ from those obtained in Experiment 2, as high-value items do show increased recollection, but not increased familiarity.

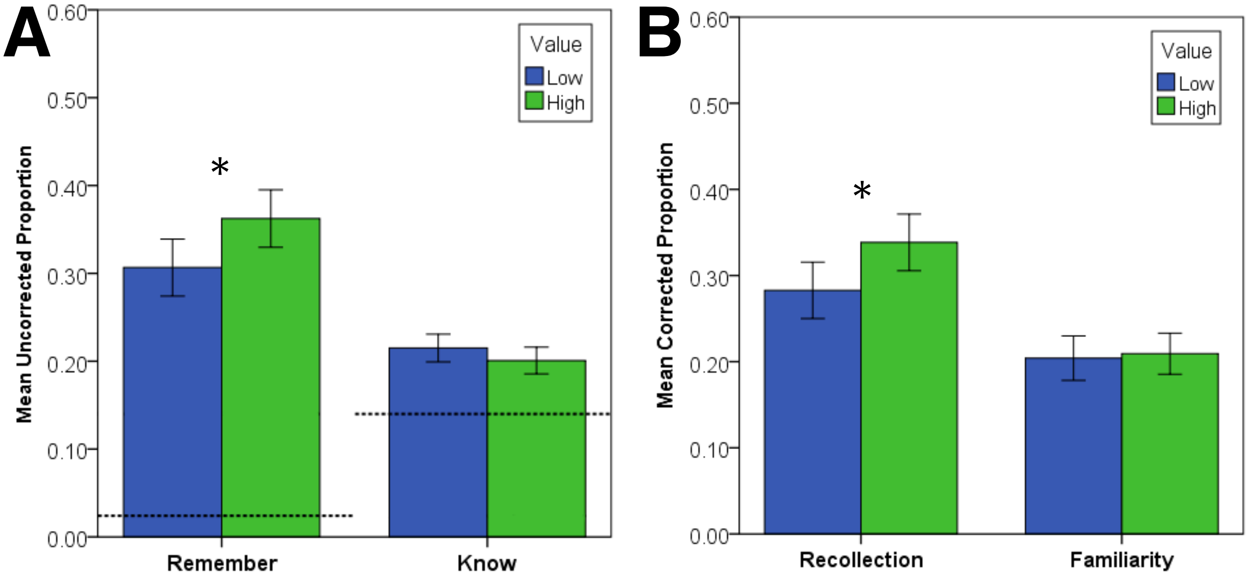

Figure 4.16. Effects of value on (A) raw proportion of R and K responses, and (B) corrected recollection and familiarity estimates, in Experiment 3. Error bars represent +/- 1 SE.

Comparison across experiments. In order to directly compare effects of value on the recognition test both with and without free recall tests, we compare the data from Experiments 2 and 3 using 2 x 2 (value x experiment) mixed ANOVAs with repeated measures on the second factor. As discussed above, it seems likely that it is appropriate to correct to an independence assumption, and thus, for simplicity, we limit both this and the following analysis to corrected process estimates. However, it does still seem worthwhile to examine all items and non-recalled items from Experiment 2 separately. We find that recollection estimates are significantly reduced in Experiment 3 compared to Experiment 2, both when all items from Experiment 2 were included, $F(1, 87) = 18.31$, $p < .001$, $\eta_p^2 = .17$, and when only non-recalled items from Experiment 2 were included, $F(1, 87) = 7.29$, $MSE = .008$, $p = 008$, $\eta_p^2 = .08$. Similarly, familiarity estimates were reduced in Experiment 3 compared to Experiment 2, both when all items from Experiment 2 were included, $F(1, 87) = 7.81$, $MSE = .011$, $p = .006$, $\eta_p^2 = .08$, and when only non-recalled items from Experiment 2 were included, $F(1, 87) = 7.51$, $MSE = .009$, $p = .007$, $\eta_p^2 = .08$. A 2 x 2 x 2 (process x value x experiment) ANOVA confirms that when considering all items from Experiment 2, there is a value x experiment interaction across processes, $F(1, 87) = 19.74$, $MSE = .016$, $p < .001$, $\eta_p^2 = .19$, but no 3-way (process x value x experiment) interaction, $F(1, 87) = 2.75$, $MSE = .009$, $p = .101$, $\eta_p^2 = .03$, although if anything, there is a trend for the value x experiment interaction to be larger for recollection. When considering only non-recalled items, there is a value x experiment interaction across processes, $F(1, 87) = 12.46$, $MSE = .010$, $p = .001$, $\eta_p^2 = .13$, and in this case, no trend towards a 3-way interaction, $F(1, 87) < 1$. Thus, while the more notable change between experiments, from a dual-process perspective, seems to be the change from having some effect of value on familiarity to having no effect of value on familiarity, there is also a reliable reduction on the effect of value on recollection that is of similar magnitude to the reduction in the effect of value on familiarity. Thus, an alternative explanation that the effects of value on memory are generally reduced when no free recall tests are administered, regardless of process dissociations, is also a possibility.

Individual differences in strategy use. As in Experiment 2, we also wanted to examine how individual differences in strategy use affect value-related changes in process estimates. In this experiment, 22 individuals were assigned to the low strategy use group. An additional 19 individuals were assigned to a combined medium/strong group; it was necessary to create a combined group because, in this experiment, only two individuals gave responses that would justify being included in a strong study group, which would not have provided sufficient power for analyses. Finally, 5 individuals did not provide sufficient information for them to be assigned to a strategy use group, and were thus excluded from these analyses.

As noted above, we only ran this analysis using corrected process estimates. For individuals in the low strategy use group, there was no effect of value on recollection, $t(21) = 1.19$, $p = .248$, nor was there an effect of value on familiarity, $t(21) = 1.27$, $p = .22$ (Figure 4.17). A 2 x 2 (process x value) within-subjects ANOVA showed a marginal trend for a process x value interaction, $F(1, 21) = 3.55$, $MSE = .003$, $p = .074$, $\eta_p^2 = .15$, likely driven by the fact that the nonsignificant trends that are present go in opposite directions, with a trend towards a positive effect of value on recollection but a trend towards a reverse value effect on familiarity. For individuals in the moderate/strong strategy group, there was an effect of value on recollection, $t(18) = 3.77$, $p = .001$, but not on familiarity, $t(18) < 1$ (Figure 4.17). Here, the process x value interaction was significant, $F(1, 18) = 11.11$, $MSE = .003$, $p = .004$, $\eta_p^2 = .38$. We also examined whether effects of value on process estimates differed across strategy use groups, running separate 2 x 2 (value x strategy group) ANOVAs for each process. The value x strategy group interaction is significant for recollection, $F(1, 39) = 8.35$, $MSE = .005$, $p = .006$, $\eta_p^2 = .18$, indicating that the effect of value on recollection is significantly larger in the moderate/strong group. The value x strategy group interaction is not significant for familiarity, however, $F(1, 39) = 2.18$, $MSE = .006$, $p = .148$, $\eta_p^2 = .05$.

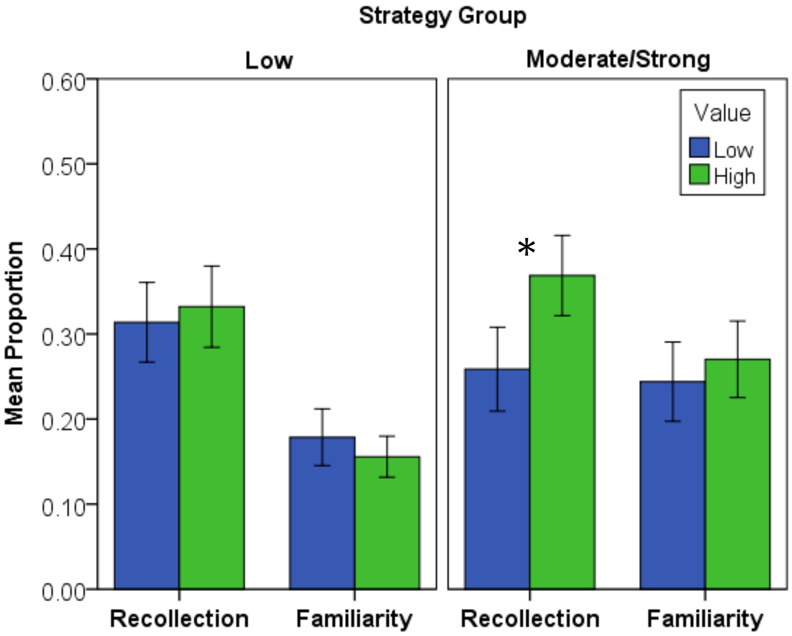

Figure 4.17. Effects of value on corrected recollection and familiarity estimates in Experiment 3, split based on assignment of participants to strategy groups based on post-study questionnaires. Error bars represent +/- 1 SE.

Discussion

When participants are presented with values at encoding, but are not preparing for free recall tests or given any sort of feedback to encourage the use of metacognition to develop strategies for utilizing those values, it seems that value still leads to increased recollection, although the effects on recollection are reliably smaller under these circumstances than when free recall tests with feedback were included. In addition, value no longer has any reliable effect on familiarity under these conditions. These results are consistent with the idea that value is affecting memory via automatic mechanisms, which tend to enhance recollection while not affecting familiarity, rather than via the use of strategies that lead to deeper encoding, which are more likely to affect both recollection and familiarity.

The effects obtained when splitting the sample by self-reported strategy use are also notable. Specifically, it seems that, unlike in Experiment 2, in which value tended to affect recollection regardless of self-reported strategy use, the influence of value on recollection varied by self-reported strategy use, as only people who claimed have at least some explicit sensitivity to value showed any reliable effect of value on recollection. It may be when recall practice and feedback is provided in Experiment 2, even people who claim to not care about value are at least sensitive to it on an implicit level, and show non-strategy-driven effects of value on memory. Under the conditions of Experiment 3, however, value is never made motivationally salient, and thus individuals who claim to be insensitive to value may in fact be ignoring value entirely. Thus, we can conclude that value needs to be motivationally salient in order to have even implicit/automatic effects on encoding.

In contrast, individuals who claim to be sensitive to value show reliable effects of value on recollection but not on familiarity. This again differs from Experiment 2, in which people in both the moderate and strong strategy use groups showed effects of value on both processes. One possible explanation for this finding is that, without practice and feedback to help people use metacognition to develop strategies, even people who are motivated to utilize value at encoding will not apply strategies differentially. The fact that value does enhance recollection in these individuals may be because value is motivationally salient for them, and thus value will enhance memory via automatic mechanisms. Still, those automatic effects of value on memory are not able to enhance memory for high-value items to the degree that is possible via selective strategy use, and in particular, they seem to only enhance recollection, not familiarity.

Experiment 4

One potential concern with interpreting the results of Experiment 2 is that the critical results, particularly those relating to familiarity, are only found when the Remember/Know results are corrected to assume that recollection and familiarity are independent processes. Given that this assumption is controversial, it seemed advisable to try to replicate our findings using a task dissociation procedure, which is a way to dissociate factors that influence recollection and familiarity without requiring assumptions about the relationship between the two processes. One way that prior literature has used to do this is to vary whether items are presented in plural or singular form (e.g., Hintzman, Curran, & Oppy, 1992). Remembering plural status has been shown to require recollection; however, the ability to access a familiarity-based memory that some form of a given word was presented tends to be available more quickly than recollection can occur (Hintzman & Curran, 1994; Curran, Tepe, & Piatt, 2006). Thus, one way to assess recollection is to use a forced-choice recognition test that requires distinguishing between the plural and singular forms of the tested word. A related means of assessing familiarity is to use a speeded forced-choice test in which the lure words were not seen during the study, with a limited enough response window that subjects do not have time to access recollection. This is the basic procedure that we use in Experiments 4, 5, and 6.

Method

Participants. Data are reported from 64 individuals recruited from the UCLA undergraduate student subject pool. An additional 6 individuals participated in the study, but they were replaced, 5 due to computer errors that interfered with completion of the study, and 1 due to an experimenter error.

Materials. The words for study that met the same criteria as other items used throughout this set of studies. However, it was also necessary that all words that were either learned during the encoding task or used as lures have a reasonable plural form; thus, some of the specific words used in this task were changed compared to prior experiments. In addition, because only half of the words were to be included in any given test, we decided to add an additional list to the experiment, making for 8 lists of items instead of 7. Thus, 192 words were studied during the encoding phase, of which 168 were tested during the later recognition test, half in the plurals test and half in the speeded item recognition test. An additional 84 words, meeting the same psychometric criteria as the studied words, were used as lures for the speeded test.

Procedure. The procedure for each trial was essentially the same as that used in Experiment 2. However, words were presented in either singular or plural form, and participants were instructed that on the free recall tests, they would be required to recall each item in the correct plural or singular form in order to get credit for that item. Indeed, the feedback provided only counted items that were recalled in the correct plural or singular form. However, items that were recalled in the incorrect form were indicated as such on the scoring sheet, and for any analyses in which recalled items are excluded, items that were recalled with incorrect plural status are also excluded.

During the recognition test, half of the participants were given the plurals test first, while half were given the speeded test first. Each test began with instructions and included 4 practice items. After the practice items, participants were given an opportunity to ask the experimenter questions; then, the experimenter typically left the room. Each test included 84 pairs of words, with one word presented on the right side of the screen and one word presented on the left side of the screen. Participants were instructed to press the "m" key, on the right side of the keyboard, if they had previously studied the word on the right side of the screen, and to press the "z" key, on the left side of the keyboard, if they had studied the word on the left side of the screen.

For the plurals test, both the singular form and the plural form of the word were presented on-screen, and the participant was given up to 6 seconds to choose which one they had seen before. For the speeded item test, the presented item and an unrelated lure were presented for 750 ms, with the lure word always presented in the same plural form as the corresponding old word. In both tests, the response needed to be made while the item was still on the screen. If the allocated presentation time passed without a response being entered, the screen displayed the message, "Too slow! Please respond faster next time" for 2 s. After a response was made, the words immediately disappeared from the screen. Following either a response or the appearance of the "Too slow" screen, a blank screen came up for the next 1.5 s, after which the next word would be presented. The order of items within each test was randomized independently by the computer for each subject. After each third of the test, i.e., after each 28 items, a screen came up that allowed the participant to take a short break, if desired; they could then press a key to resume the test. After the first recognition test was complete, instructions were provided on-screen for the second test, along with 4 additional practice items. Then, the participant went on to complete the other type of recognition test. Finally, a post-study questionnaire was completed at the end, which would again allow us to divide participants by how strongly they made use of strategies.

The presentation duration for the speeded test was chosen to be just fast enough to allow for some recognition by familiarity, while being too short to allow for recollection. As will be apparent from the results below, accuracy on this test was only barely above chance, and subjects also often complained that they had great difficulty answering within the allotted time. Thus, it seems that we were successful in choosing a response duration at the limit of young adults' capabilities.

The paradigm used in this and the following experiments included 16 counterbalancing conditions. The following factors were counterbalanced across participants: assignment of items to value groups (high or low) at encoding, the plural status of a given word (singular or plural), the assignment of item to the type of recognition test (plurals or speeded item test), and which test was presented first (plurals or speeded item test). In addition, across all items, the correct item was equally likely to be on the left side or the right side of the screen, although the assignment of item to side was not fully independent of other factors. That is, for half of the words, the plural form was always on the left when it was the correct answer and the singular form was always on the right when it was the correct answer, while this ordering was reversed for the other half of the words. Given that this factor was counterbalanced across items, and plural status was counterbalanced across subjects, the design would seem to be sufficient to equate for any differences as a function of presentation hemisphere for a given item. Note as well that the same 84 words were used as lures on the speeded item test across conditions, regardless of which half of the items presented during the encoding phase were included on that recognition test. This means that each lure was paired with one old word for half of the participants and with a different old word for the other half of the participants.

Results

Free recall. First, we examine how value affects performance on the initial free recall test, averaging across lists 2 through 8. When only items that were recalled in the correct plural/singular form are considered, the proportion of items recalled is higher for high-value items than for low-value items, *t*(63) = 13.17, *p* < .001 (Figure 4.18). Similarly, more items are also recalled in the incorrect plural form for high-value items than for low-value items, *t*(63) = 6.81, *p* < .001 (Figure 4.18). Finally, when a lenient recall score is computed, based on the combined total of recalled items regardless of plural status, there is also a significant advantage for high-value words, *t*(63) = 13.25, *p* < .001. We can also assess the effect of value on recall via selectivity index. The mean selectivity index across lists 2-8 is significantly greater than zero whether recall is scored strictly, *t*(63) = 14.04, *p* < .001 or scored leniently, *t*(63) = 13.92, *p* < .001.

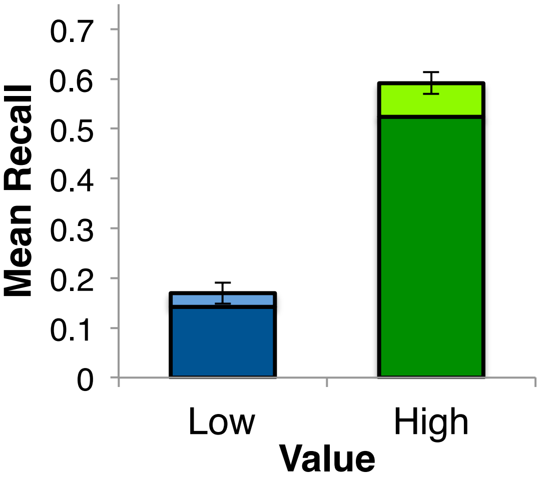

Figure 4.18. Free recall performance for high-value and low-value items in Experiment 4. Dark portions of each bar represent items that were fully correct, including plural or singular form, while lighter portions of each bar represent additional items that were recalled but in the incorrect plural form. Error bars represent +/- 1 SE computed based on lenient scoring procedures.

Recognition data. Similar to Experiments 1 and 2, we score the recognition data in this experiment separately for all items and for non-recalled items. Note that items for which no response was provided in the allowed amount of time were excluded from the analysis, as were all items with a reaction time (RT) less than 50 ms. When considering all other items, regardless of whether they were recalled on one of the initial free recall tests, we find a significant effect of value on value on the plurals test, $t(63) = 6.47$, $p < .001$. There is also a trend towards an effect of value in the speeded item test, $t(63) = 1.66$, $p = .101$, but this is not significant. A 2 x 2 (process x value) within-subjects ANOVA finds that the process x value interaction is significant, $F(1, 63) = 11.11$, $MSE = .007$, $p = .001$, $\eta_p^2 = .15$ (Figure 4.19A). When only items that were not recalled during the free recall test are included in the analysis, we again see a significant effect of value on the plurals test, $t(63) = 3.21$, $p = .002$, as well as a marginal effect of value on the speeded items test, $t(63) = 1.73$, $p = .088$, but there is not a significant process x value interaction, $F(1, 63) < 1$ (Figure 4.19B). Thus, if we assume that performance in the plurals test reflects recollection, we again find that high-value items are more likely to be recollected than low-value items, regardless of

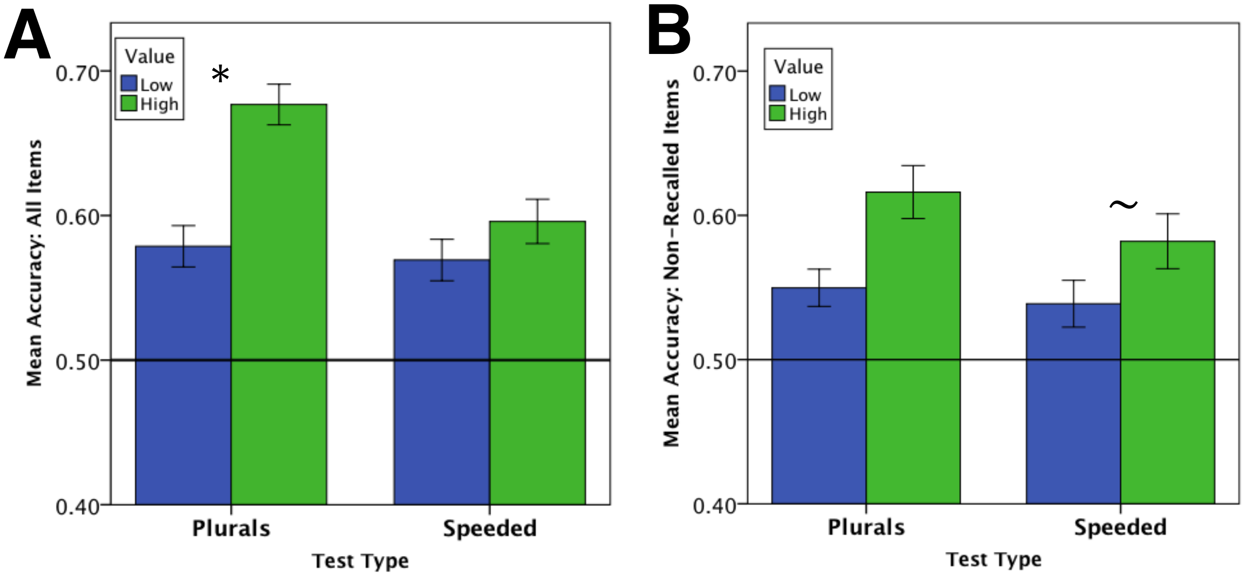

Figure 4.19. Effects of value on accuracy in plurals vs. speeded recognition test, using (A) All items, and (B) Non-recalled items, in Experiment 4. The black line at 50% represents chance performance. Error bars represent +/- 1 SE.

whether an item was freely recalled earlier. At the same time, when looking at performance on the speeded item test, which is believed to rely selectively on familiarity processes, the effect of value on memory performance is marginal. Thus, this study alone is not able to either support or disconfirm the result from Experiment 2, by which high-value items show an increase in familiarity as well as recollection.

Individual differences in strategy use. As before, it is also possible to try to determine how individual differences in self-reported strategy use relate to performance on the different recognition tests. First, we look at how differences in strategy use are associated with performance on the free recall test (Figure 4.20). When using strict scoring, people in the low strategy use group show a significant effect of value on recall, $t(10) = 2.29$, $p = .045$. In the moderate strategy group, there is a highly significant effect of

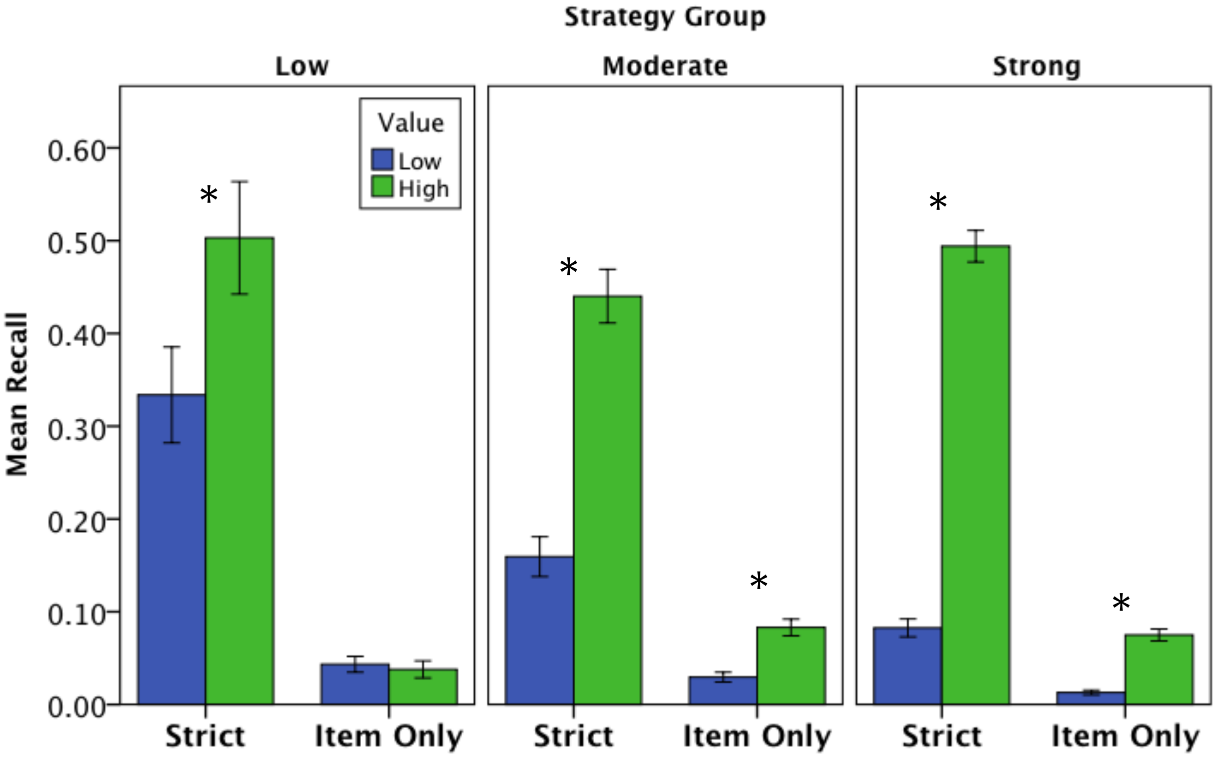

Figure 4.20. Effects of value on the proportion of items that people correctly recalled on the free recall test, in the correct plural form (Strict), and in the incorrect plural form (Item only), split by self-reported strategy use group. Error bars represent +/- 1 SE.

value on recall, $t(20) = 7.55$, $p < .001$, and the same is true for the strong strategy group, $t(31) = 15.30$, $p < .001$. A 2 x 3 (value x strategy group) mixed ANOVA with repeated measures on the first factor confirms that there is an interaction between value and strategy group on strictly-scored recall, $F(2, 61) = 15.35$, $MSE = .013$, $p < .001$, $\eta_p^2 = .34$, in that effects of value get stronger as self-reported strategy use becomes stronger.

We can also look at how self-reported strategy use changes how value affects the proportion of items which people get correct without the correct plural status. Recalling an item, but getting the critical source detail incorrect, could be considered a measure of familiarity. For the low strategy use group, there is no effect of value on recall in this category, $t(10) < 1$, but for individuals in the moderate strategy group, $t(20) = 3.84$, $p = .001$, and for individuals in the strong strategy group, $t(31) = 6.77$, $p < .001$, high-value items are more likely than low-value items to be recalled without correct plural status (Figure 4.20). There is a significant value x strategy group interaction, $F(2, 61) = 7.03$, $MSE = .002$, $p = .002$, $\eta_p^2 = .19$, indicating that the effect of value on item recall without source does differ between groups. Post-hoc Tukey tests show that this difference is significantly different between the low and moderate strategy groups, $p = .023$, and between the low and strong strategy group, $p = .001$, while there is no reliable difference between the moderate and strong strategy groups, $p = .542$. Additionally, there are interactions such that effects of value on recall are stronger for strict recall than for item-only recall in all groups: in the low strategy use group, $F(1, 10) = 6.13$, $MSE = .004$, $p = .033$, $\eta_p^2 = .38$, in the moderate strategy use group, $F(1, 20) = 44.38$, $MSE = .008$, $p < .001$, $\eta_p^2 = .69$, and in the strong strategy use group, $F(1, 31) = 142.20$, $MSE = .007$, $p < .001$, $\eta_p^2 = .82$.

In addition, in the low strategy use group (M = .145, SD = .186), selectivity index based on strictly scored recall is significantly greater than zero, t(10) = 2.58, p = .027. Selectivity is also significantly greater than zero in the moderate strategy group (M = .469, SD = .261), t(20) = 8.25, p < .001, and in the strong strategy group (M = .631, SD = .207), t(31) = 17.20, p < .001. One-way ANOVAs confirm that there is a significant effect of strategy use on selectivity index, F(2, 61) = 19.63, MSE = .05, p < .001, η_p^2 = .39, and post-hoc Tukey tests confirm that the low strategy group had lower selectivity than either the moderate strategy group, p = .001, or the strong strategy group, p < .001, while the moderate strategy group had lower selectivity than the strong group as well, p = .032.

Effects of strategy group on recognition results are not as easily interpretable in this experiment as they are in Experiment 2 and 3 (Table 4.1). In the low strategy use group, when considering all items, we find a marginal effect of value on recollection, t(10) = 1.85, p = .094, and no effect on familiarity, t(10) < 1, but also no interaction between value and process, F(1, 10) = 1.93, MSE = .007, p = .195, η_p^2 = .16. For non-recalled items, we do not find an effect of value on recollection, t(10) = 1.14, p = .279, or an effect of value on familiarity, t(10) = 1.24, p = .242, as well as no interaction between value and process, F(1, 10) < 1. In the moderate strategy use group, with all items, there is a significant effect of value on recollection, t(20) = 4.90, p < .001, but no effect of value on familiarity, t(20) = 1.02, p = .32, and the value x process interaction is also significant, F(1, 20) = 10.00, MSE = .004, p = .005, η_p^2 = .33. Similarly, for non-recalled items in the moderate strategy group, there is an effect of value on recollection, t(20) = 3.65, p = .002, but no effect of value on familiarity, t(20) < 1, and the value x process interaction is significant, F(1, 20) = 5.87, MSE = .009, p = .025, η_p^2 = .23. Finally, for the strong strategy use group, with all items, there is a significant effect of value on recollection, $t(31) = 4.21$, $p < .001$, but no effect of value on familiarity, $t(31) = 1.46$, $p = .154$, and a marginal interaction between process and value, $F(1, 31) = 3.20$, $MSE = .010$, $p = .084$, $\eta_p^2 = .09$. However, for non-recalled items, there is not a significant effect of value either on recollection, $F(1, 31) < 1$, or on familiarity, $F(1, 31) < 1$. Finally, there are no interactions between value and strategy group for recollection in all items, $F(2, 61) < 1$, or for familiarity in all items, $F(2, 61) < 1$. There is a marginal trend towards a value x strategy group interaction for recollection in non-recalled items, $F(2, 61) = 2.72$, $MSE = .013$, $p = .074$, $\eta_p^2 = .08$, which is driven by the fact that the effect of value on recollection is significant only for the moderate strategy use group, but there appears to be no such trend for familiarity in non-recalled items, $F(2, 61) < 1$.

Table 4.1. Mean proportion correct on plurals test (recollection) and speeded item test (familiarity), split by strategy groups, in Experiment 4. Cells reflecting significant value effects are bolded.

Strategy	Low (n = 11)		Moderate (n = 21)		Strong (n = 32)	
Value	High	Low	High	Low	High	Low
Plurals (All Items)	.732	.667	**.697**	**.583**	**.645**	**.546**
Plurals (Non-recalled)	.655	.596	**.682**	**.550**	.560	.534
Speeded (All items)	.660	.664	.588	.557	.579	.545
Speeded (Non-recalled)	.654	.543	.575	.547	.562	.532

Discussion

Using a task dissociation method to separate recollection and familiarity, we replicate the finding from earlier experiments that high-value items are more likely to be recollected, in terms of being able to distinguish between plural and singular forms of a studied word, even when non-recalled items are excluded. On the speeded test, intended to assess familiarity, we found a marginal trend towards a beneficial effect of value across all subjects, but this effect was not significant. Thus, the trends are consistent with the idea that high-value items in the value-directed remembering paradigm show an increase in both recollection and familiarity, but it is not a conclusive replication of Experiment 2.

Another novel finding is that people are able to encode source information, specifically, the plural status of the presented words, in the context of the value-directed remembering task. At the same time, high-value items were more likely to be recalled in the incorrect plural form than were low-value items, in addition to being much more likely to be recalled using the correct plural form. This is in contrast to the effects of value shown by Shigemune et al. (2014) and by Gruber et al. (2015), who found effects of value on the rate of source-accurate item recall, but not on the rate of recall for items without accurate source information, when value affects memory via an automatic, dopamine-driven mechanism. If we can assume that recall of an item in the incorrect plural form will depend largely on familiarity, this finding constitutes a replication of one of the key findings from Experiment 2. That is, it seems that high value enhances both recollection and familiarity when combined with the opportunity for practice and feedback that is central to the value-directed remembering paradigm, in contrast to the specific enhancement for recollection found with purely reward-based manipulations.

It is also notable that effects of value on item recall without source are only found in participants who reported being sensitive to value. In people who self-report being indifferent to value, there is still a significant effect of value on memory with accurate source encoding, presumably driven by recollection, but there is no effect of value on item memory without source, which is presumably driven by familiarity. This provides a further replication of a key finding from Experiment 2, which is that individuals who are not explicitly sensitive to value see an enhancement only in recollection, likely driven by implicit mechanisms, while individuals who are explicitly sensitive to value show increases in both recollection and familiarity-driven memory.

In contrast to what we find in the recall data, the results of the split by strategy group in terms of the plurals and speeded recognition test were not particularly informative. Given that, in Experiment 2, effects of value on familiarity were reliably stronger for individuals who reported strongly varying encoding as a function of strategy use, one possibility was that the analogous subset of participants would show significant effects of value on the speeded test in this study. However, this does not appear to have been the case. There were also other odd results, such as individuals in the moderate strategy group having had the strongest effects of value on recollection, while individuals in the strong strategy group did not show any effects of value on recollection when recalled items were removed. One possibility is that, with so many different potential confounds that needed to be counterbalanced, the subset of subjects who reported using similar strategies did not get the benefit of the counterbalancing. Another possibility is that both the all-item and the non-recalled item analyses are too biased to give clear results when value effects are relatively small to begin with. Experiment 5 addresses this latter possibility.

Experiment 5

In Experiments 1, 2, and 4, it was necessary to separately examine effects of value both on all items and on non-recalled items. However, both approaches could be considered problematic. An analysis including all items could have memory for freely recalled items boosted by memory for the recall test, but an analysis including only non-recalled items eliminates some items that would be remembered on the recognition test, which could bias the results in a different way. Particularly given the uncertainty of the replicability of the effect of value on familiarity across procedures, between Experiment 2 and Experiment 4, we hoped that correcting for the issue of having to either include or exclude freely recalled items would lead to cleaner results. At the same time, Experiment 3 demonstrates that the effects of value get notably weaker, and likely change in terms of dual-process character, when no free recall tests are included. Thus, in order to show the encoding processes that are typical in the value-directed remembering paradigm, it was necessary for participants to expect the possibility of a free recall test, and to get such a test on some lists. Thus, in this version of the paradigm, we repeated the paradigm used in Experiment 4, except that participants were only given free recall tests on 3 of the 8 lists. This meant that items from the other 5 lists could be analyzed without contamination from having completed a free recall test on those items.

Method

Participants. Data from 48 students from the UCLA psychology department undergraduate subject pool are reported in this study. An additional 1 subject was run, but this individual could not complete the experiment due to a computer failure and was replaced.

Materials and Procedure. The materials and procedure were identical to those used in Experiment 4, except that, as noted above, free recall tests were only presented on 3 of the 8 lists. The first list, for which items were never included in the recognition test in any of the experiments presented in this chapter, was always given a free recall test. After that, the computer randomly chose one list out of lists 2-4 to get the second free recall test, and randomly chose one of lists 5-8 to get the third free recall test. Participants were not informed about how the tested lists would be chosen, but were told that some lists would have a recall test and some lists would not. They were also reminded to always study the words as if they were going to have a recall test on that list. Participants were not told whether there would be a test on a given list until presentation of that list was complete. If there was to be a test, the instructions for the test would be displayed, otherwise a message would be displayed saying that "you will not be tested on this list," and the participant could then press a key to continue to the next list. Participants were also not told about the recognition test in this experiment until immediately before it began.

Results

Free recall. Although recall tests were only given on three lists, this is still enough data to confirm that value affected free recall in the expected ways. For consistency with previous experiments, we also do not include scores from the recall test in list 1. Thus, scores presented here are based on the 2 lists that were tested out of the final 7 lists. Using strict scoring, the proportion of high-value items recalled (M = .459, SD = .184) was higher than the analogous proportion for low-value items (M = .096, SD = .093), $t(47) = 11.07$, $p < .001$. Similar results were obtained when considering only items that were recalled in the incorrect plural form, with a higher proportion of high-value items (M = .065, SD = .045) than low value items (M = .018, SD = .028) being in this state, $t(47) = 6.52$, $p < .001$. Finally, the totals computed using lenient scoring, combining items recalled regardless of plural status, also show better recall for high-value items, (M = .524, SD = .173) than low-value items (M = .115, SD = .108). In addition, selectivity indices computed using data from those same two lists were significantly greater than zero, whether using strict scoring M = .582,

$SD = .291$, $t(47) = 13.84$, $p < .001$, or using lenient scoring $M = .592$, $SD = .287$, $t(47) = 14.28$, $p < .001$.

Recognition test. The primary reason for running this experiment was to determine how value affected recollection and familiarity when they were completely uncontaminated by a recall test. Using data from the 5 lists that were not tested, we find a reliable effect of value on the plurals test (recollection), $t(47) = 4.79$, $p < .001$, but no effect of value on the speeded test (familiarity), $t(47) = 1.26$, $p = .22$, and a significant process x value interaction, $F(1, 47) = 6.37$, $MSE = .010$, $p = .015$, $\eta_p^2 = .12$ (Figure 4.21A).

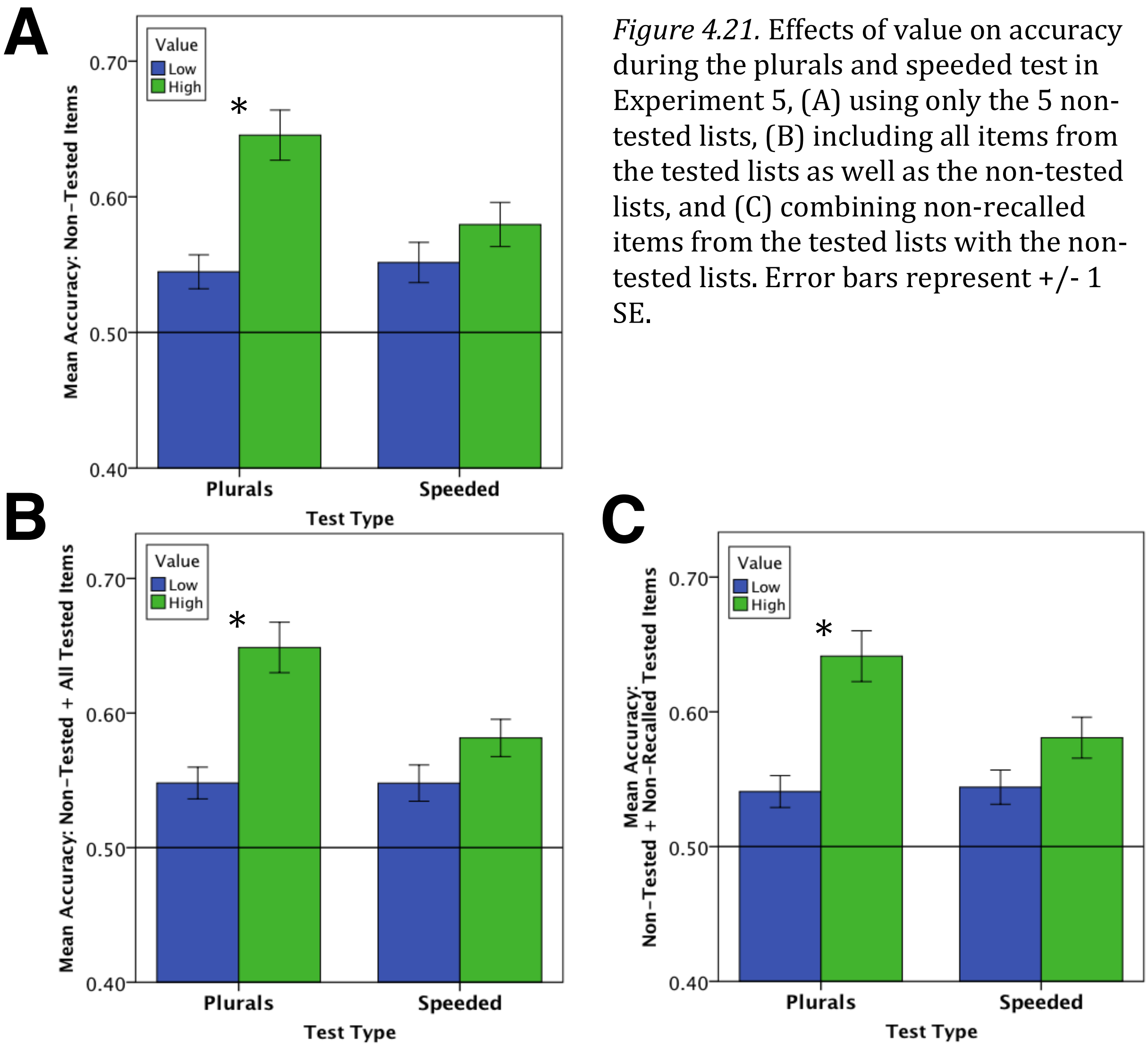

Figure 4.21. Effects of value on accuracy during the plurals and speeded test in Experiment 5, (A) using only the 5 non-tested lists, (B) including all items from the tested lists as well as the non-tested lists, and (C) combining non-recalled items from the tested lists with the non-tested lists. Error bars represent +/- 1 SE.

While the effect of value is clearly larger on recollection than on familiarity in the above analysis, there is still a trend for a positive effect on familiarity. One way to increase statistical power to try to find such an effect is to re-run the analysis, combining the 5 non-tested lists either with all items, or with the non-recalled items, from the 2 tested lists out of lists 2-8. When considering all items, there is an effect of value on recollection, $t(47) = 5.00$, $p < .001$, but only a marginal effect on familiarity, $t(47) = 1.79$, $p = .081$, and the process x value interaction is again significant, $F\ (1, 47) = 5.96$, $MSE = .009$, $p = .018$, $\eta_p^2 = .11$ (Figure 4.21B). Finally, when considering only non-recalled items, we again see an effect of value on recollection, $t(47) = 4.97$, $p < .001$, a marginal effect of value on familiarity, $t(47) = 1.81$, $p = .076$, and a process x value interaction, $F\ (1, 47) = 5.02$, $MSE = .010$, $p = .030$, $\eta_p^2 = .10$ (Figure 4.21C).

There is one final way by which it could make sense to increase power, which is to combine data from the present experiment with data from Experiment 4. In doing so, it would seem to make the most sense to again combine data from the two lists that were tested in Experiment 5 with the 5 lists that were not tested, and again separate out the analysis for all items vs. non-recalled items. Each lower-level analysis was run as a 2 x 2 (value x experiment) mixed ANOVA with repeated measures on the first factor, while 2 x 2 x 2 (process x value x experiment) mixed ANOVAs were used to assess process x value interactions. Including experiment as a factor in the statistical model allows us to determine whether any observed effects are indeed present across both experiments, or whether there may be an interaction with experiment. For all items, we find a significant effect of value on recollection, $F(1, 110) = 64.70$, $MSE = .008$, $p < .001$, $\eta_p^2 = .37$, as well as a significant effect of value on familiarity, $F(1, 110) = 5.97$, $MSE = .008$, $p = .016$, $\eta_p^2 = .05$, and the process x value interaction is also highly significant, $F(1, 110) = 16.28$, $MSE = .008$, $p < .001$, $\eta_p^2 = .13$. For non-recalled items, we see a similar pattern of effects: a significant effect of value on recollection, $F(1, 110) = 31.76$, $MSE = .012$, $p < .001$, $\eta_p^2 = .22$, and a significant effect of value on familiarity, $F(1, 110) = 5.59$, $MSE = .016$, $p = .020$, $\eta_p^2 = .05$. Here, the process x value interaction is marginally significant, $F(1, 110) = 3.49$, $MSE = .015$, $p = .064$, $\eta_p^2 = .03$. None of these effects showed any hint of an interaction with experiment; all $F(1, 110) < 1$, with the exception of a weak trend for a value x experiment effect on recollection for non-recalled items, $F(1, 110) = 1.33$, $MSE = .012$, $p = .252$, $\eta_p^2 = .01$, and we might in fact expect an interaction with experiment on that measure, given that in Experiment 5, the non-recalled items measure includes many non-tested items that would have been recalled, and thus excluded from this measure, under the procedures used in Experiment 4. Thus, we can conclude that, as was suggested by the trends that were apparent when looking separately at Experiment 4 and 5, it is possible to see an effect of value on the speeded recognition test with a large enough sample size.

Individual Differences in Strategy Use. We again examine how individual differences in self-reported strategy use relate to memory performance (Table 4.2). Because only 3 individuals in Experiment 5 reported being indifferent to value, we did not run statistics on the low strategy use group, although we do report means in Table 4.2. The remaining groups, moderate and strong strategy use, are somewhat more homogeneous. Both the moderate group, $t(14) = 4.59$, $p < .001$, and the strong group, $t(29) = 12.00$, $p < .001$, show highly significant effects of value in strictly-scored recall, but a 2 x 2 mixed ANOVA shows that the effect of value is significantly stronger in the strong strategy use group, $F(1, 43) = 6.41$, $MSE = .019$, $p = .015$, $\eta_p^2 = .13$. Both the moderate group, $t(14) =$

2.69, p = .017, and the strong group, $t(29)$ = 7.48, t < .001, also show significant effects of value on the recall of items with incorrect plural status, but the value x strategy group interaction there is not significant, $F(1, 43) < 1$. It is notable that the 3 subjects who would constitute the low strategy-use group do not a value-related difference in the proportion of item-only recall, consistent with what we found in Experiment 4. Finally, the effect of value on strict recall is significantly larger than the corresponding effect on item-only recall, both in the moderate strategy use group, $F(1, 14)$ = 10.29, MSE = .016, p = .006, η_p^2 = .42, and in the strong strategy use group, $F(1, 29)$ = 112.83, MSE = .008, p < .001, η_p^2 = .80.

We also split the data from the recognition test by strategy group, although, as in Experiment 4, these data do not tell a very clear story. For the non-tested items, the moderate strategy use group does not show a reliable effect of value on recollection, $t(14)$ = 1.41, p = .180, nor is there a reliable effect on familiarity, $t(14)$ = 1.10, p = .291, and there is no process x value interaction, $F(1, 14) < 1$. When all items from the tested lists are added to the non-tested items, for this same group of subjects, there is a significant effect of value on recollection, $t(14)$ = 2.53, p = .024, and there is also a significant effect of value on familiarity, $t(14)$ = 2.60, p = .021, with no process x value interaction, $F(1, 14) < 1$. Similarly, when non-recalled items are included along with non-tested items, we see a significant effect of value on recollection, $t(14)$ = 2.59, p = .021, and a significant effect of value on familiarity, $t(14)$ = 3.14, p = .007, with no process x value interaction, $F(1, 14) < 1$.

For individuals in the strong strategy use group, non-tested items show a significant effect of value on recollection, $t(29)$ = 5.53, p < .001, as well as a significant effect of value on familiarity, $t(29)$ = 2.35, p = .026, but there is also a process x value interaction, $F(1, 29)$ = 8.09, MSE = .008, p = .008, η_p^2 = .22, such that value has a stronger effect on recollection than on familiarity. For this group, however, when all items from the tested list are added to the non-tested items, we still see a significant effect on recollection, $t(29) = 4.69$, $p < .001$, but the effect on familiarity is only marginal, $t(29) = 1.73$, $p = .095$, with a significant process x value interaction, $F(1, 29) = 7.94$, $MSE = .009$, $p = .009$, $\eta_p^2 = .22$. Similarly, when non-recalled items from the tested lists are added to the non-tested items, we see a significant effect of value on recollection, $t(29) = 4.76$, $p < .001$, but the effect on familiarity is marginal, $t(29) = 1.79$, $p = .083$, and there is a process x value interaction, $F(1, 29) = 6.90$, $MSE = .010$, $p = .014$, $\eta_p^2 = .19$.

Table 4.2. Mean proportion correct on recall, plurals test (recollection) and speeded item test (familiarity), split by strategy groups, in Experiment 5. Cells reflecting significant value effects are bolded

Strategy	Low (n = 3)		Moderate (n = 15)		Strong (n = 30)	
Value	High	Low	High	Low	High	Low
Recall (Strict)	.625	.181	**.378**	**.125**	**.483**	**.074**
Recall (Item only)	.014	.028	**.072**	**.028**	**.067**	**.013**
Plurals (Non-tested)	.544	.600	.626	.582	**.666**	**.521**
Plurals (All Items)	.579	.587	**.637**	**.576**	**.661**	**.530**
Plurals (Non-recalled)	.545	.587	**.635**	**.569**	**.654**	**.522**
Speeded (Non-tested)	.347	.612	.583	.540	**.601**	**.552**
Speeded (All items)	.436	.643	**.600**	**.519**	.587	.553
Speeded (Non-recalled)	.376	.620	**.606**	**.514**	.589	.551

Discussion

We largely replicated the effects from Experiment 4 when memory was not biased by having taken a free recall test on the same items. People are more likely to remember high-value items in the plurals test, indicating greater recollection. One novel result that is more interpretable due to the unique procedure used in Experiment 5, as compared to other experiments, is that there is a process x value interaction, such that effects of value are stronger for recollection than for familiarity. In experiment 4, this effect was reliable when considering all items, but it was not for non-recalled items, so there was no way to be sure that it was due to effects at encoding rather than to strengthening of memory for recalled items during the recall test.

On the other hand, effects of value on the speeded item test still were not reliable when examining non-tested items, suggesting that the weakness of the value effects on familiarity in Experiment 4, as measured by the speeded item recognition test, is likely not due to bias from having to either include or exclude freely recalled items. However, this experiment was also similar enough to Experiment 4 to allow us to combine data across the two experiments, and with that analysis, we did see an effect of value on familiarity, regardless of whether all items or only non-recalled items are analyzed from tested lists.

The analysis based on self-reported strategy use was limited because so few individuals reported being indifferent to value. Still, we do seem to replicate the interesting result from Experiment 4 on recall; people in the moderate and strong strategy use groups show reliable effects of value on both strict and item-only recall, consistent with what we found previously. In the 3 subjects who did report treating high-value and low-value items equally, the trends were to have better strict recall on high-value items, but no effect of value on item-only recall, which would be consistent with the effects shown in Experiment 4. As in Experiment 4, it was somewhat difficult to make sense of how the different strategy groups differed in terms of effects of value on the recognition test. The strong group showed results for the non-tested items that would be in line with our predictions, as value enhanced performance on both the plurals test and the speeded item test, but this effect is no longer significant when tested items are included. The moderate strategy group also showed effects on both recollection and familiarity, but only when tested items were included, regardless of whether all tested items or only non-recalled tested items are included. It is not clear why the moderate group did not show significant effects on either test when only considering the non-tested items.

Experiment 6

While Experiments 4 and 5 do, to a certain extent, replicate the findings of Experiment 2, another key question is whether we can replicate the findings from Experiment 3 using a method that does not require assumptions about the relationship between recollection and familiarity. In other words, we wanted to test whether, when the opportunities for practice and feedback via the free recall test are eliminated, we would again find effects on recollection but not familiarity. Thus, in this experiment, as in Experiment 3, participants did not take free recall tests during the encoding task; instead, they were told to prepare for a later recognition test. They were then presented with the two differing recognition tests that we used to assess later recollection and familiarity in Experiments 4 and 5.

Method

Participants. Data collected from 64 students who participated for course credit via the UCLA undergraduate student subject pool are included in this experiment. An additional 1 student was run but was replaced due to a computer failure.

Materials and Procedure. The items in this study were identical to those used in Experiment 4 and 5. The procedure was similar as well, except that, as in Experiment 3, instead of having a free recall test at the end of each 24-item list, participants were instructed that they "had finished learning this set of words," and were to press a key to continue on to the next set. During the initial instructions, participants were informed that they would be completing a recognition test later, in which they would have to choose between a word that they saw and a word that they didn't see, and they would get the points associated with a given word if they chose correctly. They were also told that they would need to know whether the word was plural or singular when taking the later test, in order to motivate paying attention to the plural status during encoding.

Results

Recognition data. Across all subjects (Figure 4.22), we found a significant effect of value on the plurals test, reflecting recollection, $t(63) = 2.34$, while there was no significant effect of value on the speeded item test, reflecting familiarity, $t(63) < 1$; if anything, the trend was for a negative effect of value on the speeded test in this experiment. The process x value interaction was only marginal, however, $F(1, 63) = 3.37$, $MSE = .006$, $p = .071$, $\eta_p^2 = .05$.

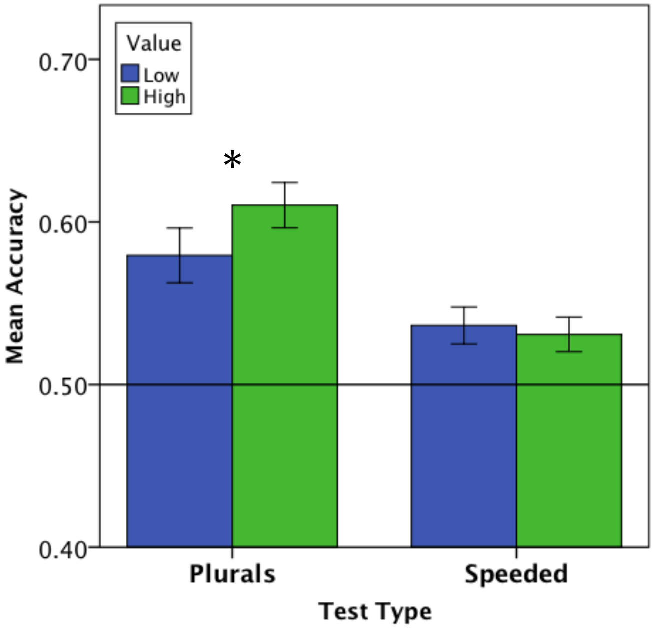

Figure 4.22. Effects of value on accuracy during the plurals and speeded test in Experiment 6. Error bars represent +/- 1 SE.

Comparison across experiments. Another way to examine how the effects of value on encoding differ based on the expectation of free recall tests is to compare results across experiments. The most appropriate comparison to Experiment 6 would seem to be the items from non-tested lists in Experiment 5. A 2 x 2 (value x experiment) mixed ANOVA, with repeated measures on the first factor, finds that there is in fact a value x experiment interaction on plurals test performance, $F(1, 108) = 7.79$, $MSE = .008$, $p = .006$, $\eta_p^2 = .07$. This means that the effect of value on recollection is significantly reduced in Experiment 6 as compared to Experiment 5. The analogous value x experiment interaction on familiarity is not significant, $F(1, 108) = 1.72$, $MSE = .009$, $p = .19$, $\eta_p^2 = .02$, indicating that the effect of value on familiarity is not significantly reduced from Experiment 5 to Experiment 6. At the same time, a 2 x 2 x 2 (value x process x experiment) mixed ANOVA finds that there is a reliable value x experiment interaction across processes, $F(1, 108) = 7.92$, $MSE = .009$, $p = .006$, $\eta_p^2 = .07$, but no 3-way interaction, $F(1, 108) < 1$, suggesting that the reduced effect of value is comparable across the two processes. Additionally, even if the quantitative reduction in the effect of value on recollection is significant, while the reduction in the familiarity effect is not, it is notable that there is a qualitative difference in how value influences familiarity across experiments, with a small but ultimately reliable beneficial effect across Experiments 4 and 5, but no hint of an effect in Experiment 6.

Individual differences in strategy use. Finally, as in the preceding experiments, we can examine how self-reported differences in how people varied encoding strategies as a function of value change the ways in which value affects memory performance. In the low strategy use group (n = 23), we find no effect of value on recollection, $t(22) = 1.68$, $p = .108$, and also no effect of value on familiarity, $t(22) = 1.19$, $p = .245$ (Figure 4.23). If anything,

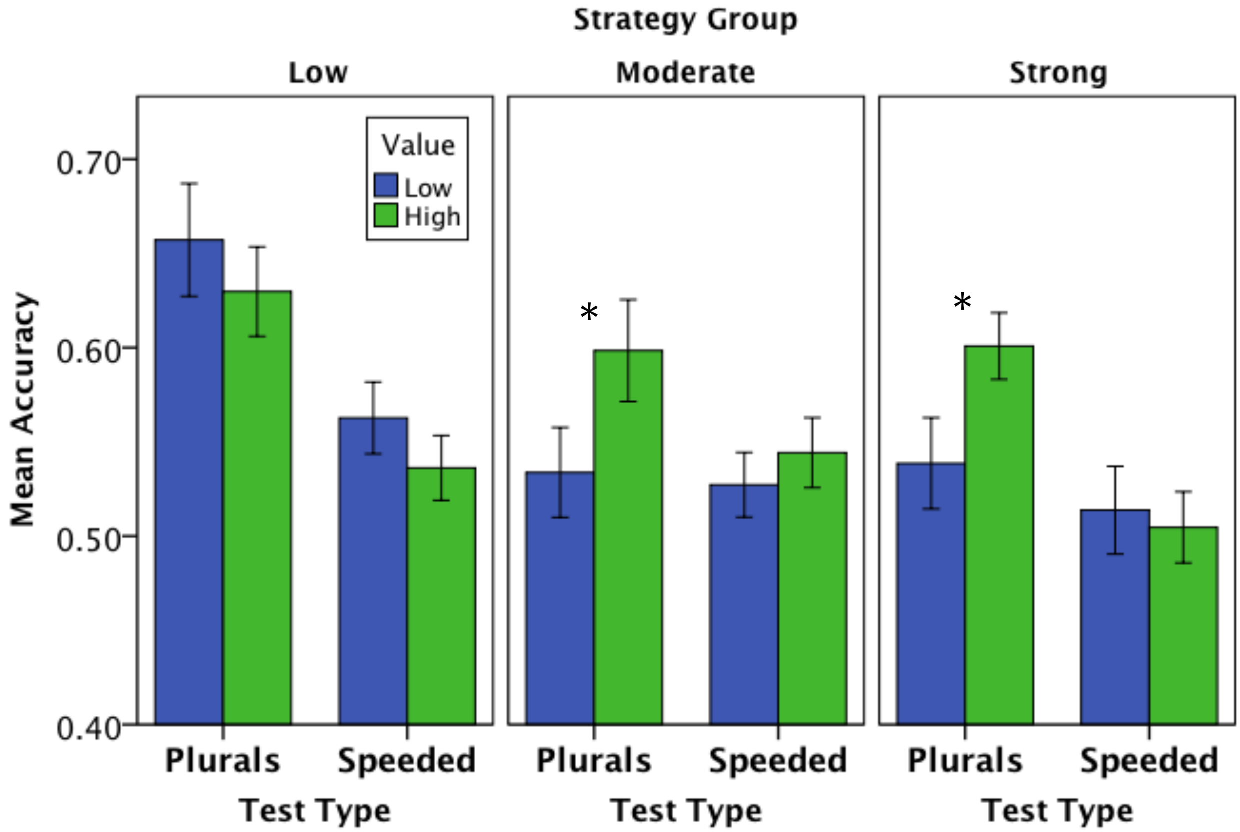

Figure 4.23. Effects of value on accuracy during the plurals and speeded test in Experiment 6, split across strategy groups. Error bars represent +/- 1 SE.

the trends for both processes are towards a negative value effect, with slightly better performance on both tests for low-value items than high-value items. There is also no process by value interaction in this group of subjects, *F*(1, 22) < 1. In the moderate strategy use group (n = 24), we find that there is a beneficial effect of value on recollection, *t*(23) = 2.78, *p* = .011, but no effect of value on familiarity, *t*(23) < 1. However, the process x value interaction is still not significant across this subset of our sample, *F*(1, 23) = 1.87, *MSE* = .007, *p* = .185, η_p^2 = .08. Finally, in the strong strategy use group (n = 17), we again find an effect of value on recollection, *t*(16) = 2.66, *p* = .017, but no effect of value on familiarity, *t*(16) < 1. Here, the process x value interaction is marginal, *F*(1, 16) = 3.14, *MSE* = .007, *p* = .095, η_p^2 = .16. We also find that the effect of value on recollection differs across the 3 strategy groups, *F*(2, 61) = 6.40, *MSE* = .005, *p* = .003, η_p^2 = .17. Post-hoc Tukey tests show that this effect is being driven by a significant difference between the low strategy use group and the moderate group, *p* = .006, and by a difference between the low strategy use group and the strong group, *p* = .015, while the moderate and strong group do not differ from each other, *p* = .997. In contrast, effects of value on familiarity do not differ between strategy use groups, *F*(2, 61) < 1.

Discussion

In this experiment, we largely replicate the pattern of effects observed in Experiment 3. Specifically, when participants are not given an opportunity for practice and feedback, we see an effect of value on recollection but not familiarity. The effect on recollection is significantly smaller than it is under similar conditions in which participants do gain experience with a free recall test (e.g., Experiment 5), but there is still an effect present. For familiarity, however, it seems that there is no hint of an effect. The effects shown here may represent the degree to which automatic/implicit effects of value can improve memory in this type of paradigm.

It is also notable that we replicate the interaction between strategy group and value that we observed in Experiment 3. Specifically, individuals who claim to be insensitive to value show no effect of value on either the recollection-based or familiarity-based test. In contrast, both groups of participants who did report paying attention to value, albeit to varying degrees, show significant effects of value on recollection, although not on familiarity. These results reinforce the idea that it is possible for people to not gain any benefits of value when practice and feedback are not available, as value can lack motivational salience for some individuals under those conditions. However, it seems that even people who do claim to care about value are only affected by it on an implicit level, as the selective application of explicit strategies should enhance familiarity as well as recollection for high-value items.

General Discussion

The work described in this chapter refines and extends the findings from the prior chapters in a number of important ways. One notable refinement is that there seems to be an additional mechanism, relative to that described in Chapters 2 and 3, by which value enhances subsequent memory. In the brain, we find negative correlations between value-related differences in activity in or near regions that are typically deactivated during successful memory encoding, and value-related differences in subsequent memory. In young adults, as shown in Experiment 1A, these value-related deactivations seem to specifically enhance recollection, and appear to be a critical means by which items that are not freely recalled, but which are still able to be recollected with a high level of episodic detail and/or confidence, are encoded.

In older adults, we also find negative correlations between value-related differences in brain activity and subsequent memory performance, but the effect is an increase in familiarity-based memory, not recollection. The nature of the effect in older adults seems somewhat more complicated than in young adults for a few reasons. The first is that the regions showing negative value effects are shifted somewhat from the regions that typically show negative subsequent memory effects. Indeed, one of the key regions showing this effect exclusively in older adults overlaps with an area of left precuneus that has previously been found to show age-dependent effects on subsequent item memory (Mattson et al., 2014), but in that study, the effect was shown in young adults but not older adults. As proposed in the Discussion to Experiment 1B, one possible way to resolve the apparent conflict is that older adults are selectively engaging a brain mechanism that they do not regularly engage, while young adults would more easily engage this mechanism spontaneously and consistently, in the same vein as what Logan et al. (2002) found in the context of levels of processing effects.

Another surprising finding is that, in older adults, there are a number of regions in which effects of value on recollection and effects of value on familiarity tend to correlate in opposite directions with effects of value on brain activity. Again, a speculative explanation could be generated. To reiterate the explanation proposed in the Experiment 1B Discussion, it is possible that the same regions that help with elaborative encoding, and that therefore help to enhance subsequent recollection, can also interfere with the engagement of lower-effort processes that lead to enhanced familiarity in older adults. Further work would be necessary to better develop this hypothesis.

Finally, it is somewhat confusing that the most theoretically interesting regions showing negative value effects in older adults do not show these effects when only non-recalled items are analyzed, despite the behavioral effects of value on familiarity being maintained when recalled items are excluded. One technical explanation is that the familiarity estimates for non-recalled items could be noisier than the estimates made for all items, due to the smaller number of old items available when recalled items are excluded. Thus, individual differences in value-related differences in those estimates may be too noisy to successfully correlate back to individual differences in brain activity. Again, replication of our findings could help to clarify this issue.

The young adult behavioral experiments that constitute Experiments 2-6 provide additional context for better understanding of the fMRI results in Experiment 1A, and a deeper understanding of the nature of the value-directed remembering paradigm more broadly. Experiment 2 found that high-value items in the value-directed remembering paradigm tend to show increases in both recollection and familiarity, specifically in participants who claim to be doing something explicitly different to try to enhance encoding of high-value items. However, this finding only emerges if the raw responses in the Remember/Know paradigm are corrected in line with an assumption of independent processes (Yonelinas & Jacoby, 1995). While the use of such a correction factor seems to be supported by prior literature (e.g., Sheridan & Reingold, 2012), we hoped to also replicate these findings using procedures that do not require assumptions about the relationship between the two processes. Indeed, although the findings from Experiments 4 and 5 are not quite as clear-cut as those in Experiment 2, it seems that in the end, we do replicate the key results. Specifically, when combining across Experiments 4 and 5 to increase power, we do see a reliable effect of value on performance in the putatively familiarity-driven speeded forced-choice recognition test, as well as an increase in performance in the putatively recollection-driven plurals recognition test.

Evidence from the recall tests in Experiments 4 and 5 support a similar conclusion. Specifically, while all groups of subjects show a strong effect of value on recall for items in the correct plural form, participants in both Experiments 4 and 5 who claim to be sensitive to value also remembered more high-value items in the incorrect plural state than they did low-value items. Presumably, these source errors reflect the rate of familiarity-driven recall, providing further evidence that value-directed encoding enhances both recollection and familiarity, at least when people are explicitly sensitive to value. Finding an effect of value on familiarity as well as recollection is informative because, as described in the introduction, manipulations of encoding strategies such as deep levels of processing and generation tend to increase both recollection and familiarity when independent processes are assumed (Yonelinas, 2002), while factors that affect memory via more automatic mechanisms, such as the dopamine-driven enhancement of memory encoding by reward, usually only increase recollection (e.g., Shigemune et al., 2014; Wittmann et al., 2011).

While the above results indicate that the typical strategy-driven mechanism underlying value-directed remembering leads to enhancement of both recollection and familiarity in a dual process analysis, it is also interesting to consider the conditions under which value instead appears to selectively enhance recollection. There are two such conditions apparent in the present series of studies. The first is in individuals who, for whatever reason, choose not to explicitly change their encoding processes for high-value items, even when free recall tests and feedback are present; that is, under conditions that lead most people to be explicitly selective in their use of strategies. In experiment 2, we found that these individuals do still show an effect of value on recollection, but, in contrast to the rest of the sample, these individuals showed no value-related increase in corrected familiarity estimates. In experiment 4, we found that a similar subgroup of individuals showed reliable effects of value on the proportion of items that they recalled with correct source information, but they showed no effects of value on the proportion of items recalled with incorrect source. In experiment 5, the number of individuals in this subgroup was too small for statistical analysis, but the numerical trends for the 3 subjects who would constitute such a group were consistent with the findings from experiment 4. In contrast, in both experiment 4 and experiment 5, the remainder of the sample showed reliable increases in both source-accurate and source-incorrect memory for high-value items.

It should be noted that in contrast to what we found in the recall tests, the pattern of effects described in the previous paragraph did not fully replicate across strategy use subgroups in the recognition tests that were originally intended to be the main behavioral measures in Experiments 4 and 5. Still, the fact that the effects replicate across both the R/K test in Experiment 2 and in the effects of source accuracy on the recall test in Experiments 4 and 5, combined with the difficulty in finding effects of value on familiarity via the speeded item recognition test even across the entire sample, suggests that the lack of replication is more likely due to the speeded item recognition test being a suboptimal measure than to a true lack of replicability of the underlying effect. In other words, it seems reasonable to speculate that because the speeded test was so fast, in order to prevent people from using recollection, the data obtained from that test are noisier and less reliable than data from measures of R/K judgments or recall source accuracy.

The other condition tested here under which value clearly shows a selective benefit for recollection is when no free recall tests are included, removing the opportunity for practice, feedback, and metacognitive control of strategy use. Specifically, in Experiment 3, high-value items were more likely to be recollected than low-value items, but familiarity estimates did not differ as a function of value, even when the Yonelinas and Jacoby (1995) correction is applied, and the value x process interaction is significant. A similar pattern was obtained in Experiment 6, as high-value items were recalled reliably better than low-value items on the plurals test, but there was no hint of a value effect on the speeded test, although the process x value interaction was only marginal. Thus, if we assume that a combined enhancement of both recollection and familiarity reflects selective use of explicit encoding strategies, while a selective enhancement of recollection alone suggests that value is enhancing memory purely by automatic mechanisms, then we can conclude that even people who do report being sensitive to value are not modulating their use of explicit strategies when preparing only for a later recognition test. In other words, it seems that some aspect of going through multiple study-test cycles during encoding, either as a function of the practice itself or of the performance-oriented feedback, is necessary to evoke the value-directed modulation of explicit strategy use that is the focus of Chapters 2 and 3 of this work.

Another notable observation from Experiments 3 and 6 is that, in both experiments, individuals who claimed not to be sensitive to value in fact showed no reliable effects of value either on recollection or on familiarity. This is distinctly different from the pattern shown in Experiments 2 and 4, and possibly Experiment 5 as well, in which individuals who claimed to be insensitive to value nevertheless do show a value-related increase in recollection. It may be that, when the value manipulation is as salient as is the case when point feedback is being provided after every list, or even after every few lists, it is unavoidable for people to at least engage low-effort, automatically-driven processes that help encoding more strongly during encoding of high-value items. In contrast, in Experiments 3 and 6, it may be that people for whom the value manipulation is not salient just “tune out” the value cues entirely, so that they do not even effect behavior on an automatic level. Further work could potentially clarify this issue.

An additional inconsistency that should be discussed here is the fact that, although the typical value-directed remembering paradigm led to a largely consistent enhancement of both recollection and familiarity across Experiments 2, 4, and 5, the ROC data analyzed in Experiment 1A did not show a reliable value-related increase in familiarity. The reason for the difference between experiments is not entirely clear, but some speculation is possible. Most notably, the number of trials available from each participant for each condition in the ROC analysis was relatively low, particularly when recalled items were excluded. Indeed, one expert in this methodology recommended to us that ROC estimates are typically not stable unless there are at least 60 trials per condition (W-C. Wang, personal communication). This is the number of trials that we had in each condition when all items were included in the analyses, but once recalled items were excluded, the trial counts were, in many cases, considerably lower. We excluded individuals with fewer than 5 non-recalled high value trials, but many of the participants whose data were included still had a relatively small number of non-recalled trials in one or both value conditions. Still, excluding more individuals would have unacceptably biased our sample towards poor performers, and in addition, the sample size for the analyses using non-recalled items was already small, with only 15 participants.

We were still able to find an effect of value on the proportion of items recollected even when looking only at non-recalled items, but prior research (e.g., Yonelinas, 2002), as well as our own results from experiments 2, 4, and 5, show that effects of value on familiarity tend to be smaller than the corresponding effects on recollection even when both effects are present. Thus, while the effect of value on recollection was strong enough to overcome degradation as a result of noisy ROC estimates and low statistical power, the effect of value on familiarity may not have been able to do so. In other words, even if there were truly an effect of familiarity on the data analyzed in Experiment 1A, our methods may not have been sensitive enough to discover it. In addition, the retention interval in the fMRI study was longer than that used in the behavioral studies, so it is possible that some items that could have been recognized using familiarity 5 minutes after study had already been forgotten by the time the recall test was administered. In any case, it seems that there are enough potential limitations with the ROC analysis that we should not overinterpret the null effects of value on familiarity in that analysis.

At the same time, the fMRI findings from Experiment 1A can inform our interpretation of the behavioral data. Specifically, it seems plausible that the automatic, low-effort mechanism that seems to underlie effects of value under the conditions tested in Experiments 3 and 6, and that also seems to underlie effects of value in participants who are less sensitive to value in Experiments 2, 4, and 5, may be driven on a neural level by the value-related reductions in default-mode activation that in Experiment 1A were shown to be particularly important for recollection in items for which free recall had failed. Further work would be necessary to test this hypothesis.

Another intriguing possibility is that the negative correlations that we find between brain activity and effects of value on familiarity in older adults reflect a similar mechanism to that showing negative correlations with recollection in young adults. It is not clear whether we might expect this to be the case, but it is at least a possibility, and it would generate some interesting and testable predictions as to what we might find when testing older adults in the types of behavioral experiments reported here. Specifically, it seems likely that in a typical value-directed remembering paradigm, in which there is an opportunity for practice and feedback, older adults would show effects of value on both recollection and familiarity. The effects of value on recollection that we observed when analyzing all items in Experiment 1B are unlikely to be entirely driven by experience on the free recall test, for the reasons discussed in the discussion to Experiment 1B. Thus, a procedure that allows one to examine non-tested items when recall tests are still part of the encoding experience, such as the procedure used at encoding in Experiment 5, should still find effects of value on recollection. However, we would also expect to find effects of value on familiarity.

More importantly, when no opportunity for practice and feedback is available, analogous to Experiments 3 and 6, we might expect to find that value affects familiarity but not recollection. Similarly, if some older adults report being insensitive to value, they could show effects of value on familiarity but not recollection even when practice and feedback is available. However, an alternate possibility under those circumstances is that, unlike young adults, the motivational salience of the value cues may not be enough to draw their attention even on an automatic level, and thus such individuals may ignore value completely, similar to the participants in Experiments 3 and 6 who were uninterested in value. If this prediction is correct, older adults who report ignoring value may not show effects of value on either recollection or familiarity.

CHAPTER 5

Conclusions and Future Directions

Summary of Findings

Across the entirety of this set of studies, a number of interesting findings are apparent. The first is that both young and older adults seem to typically be selective in applying deep semantic strategies during encoding of high-value words, in order to selectively optimize their encoding of those items. This mechanism is driven in the brain by activity in a network that includes left VLPFC/IFG, left posterior lateral temporal cortex, and pre-SMA. The fact that a similar brain network contributes to selective encoding in both age groups suggests that the circuitry of this network, or at least the ability to control the degree to which it is engaged from trial to trial, is preserved in healthy older adults. Based on the results presented in Chapter 4, it seems that a critical feature that allows the value-directed remembering to evoke this mechanism is the presence of study-test cycles that include feedback, which allow people to use metacognitive monitoring and control to adjust their encoding strategies in a way that will optimize selectivity.

Although informal observations from prior behavioral studies, such as introspective reports provided in post-study questionnaires, had given us some reason to suspect that value-related differences in the engagement of deep semantic processing at encoding underlie selectivity, it is still notable that we find evidence for such a mechanism in the brain. First, it is well-established that introspective reports cannot be trusted as reflecting objective reality, so some direct observational evidence, either from observed behavior or from observed brain activation, is necessary to confirm such a mechanistic explanation. In addition, there are some alternative explanations that we are able to at least partially rule out on the basis of these data. Specifically, one alternate possibility is that people merely engage in selective rehearsal of high-value words. It is also possible that the typically-observed effects of value on memory output are driven by dynamics of the recall test, either because people recall high-value items first and thus have trouble retrieving low-value items because of output interference, or because they suppress recall of low-value items due to demand characteristics. While we cannot rule out the possibility that such mechanisms make some contribution to selectivity, the results from this dissertation make clear that selective engagement of deeper processing of high-value items during encoding is, at the very least, a significant contributor to the effects of value on recall in the value-directed remembering paradigm, for both young adults and older adults.

We do also find evidence in the brain that young adults engage other mechanisms in addition to the modulation of controlled semantic processing during word presentation, but these mechanisms are less effective at enhancing selectivity on the recall test. Specifically, during the cues that precede presentation of high-value words, young adults show increased engagement of a network that includes semantic processing regions. However, unlike what others have shown in other task contexts (e.g., Bollinger et al., 2010; Addante et al., 2015), engagement of regions that successfully enhance encoding when engaged at a later stage of the trial does not seem to be helpful when done proactively, during a pre-stimulus cue, in this task. This null finding was particularly apparent in the recall test; in Chapter 4, Experiment 1A, we did find some weak evidence that proactive engagement of an ROI in left anterior PFC does correlate with value-related improvements in recollection on the later recognition test, but more evidence would be needed to confirm this tentative finding. In any case, older adults do not show this proactive encoding effect, suggesting either a way in which the requirements of this task happen to align with the capabilities of older adults, or, alternatively, a possible way in which older adults are being more efficient with their cognitive resources than young adults.

Young adults also show increased engagement of reward-sensitive regions for high-value items, both during the pre-stimulus cue and during the presentation of the word itself. Unlike what other studies (e.g., Adcock et al. 2006) have shown, activity in reward-sensitive regions during the cue does not enhance recall for young adults in this paradigm; analogous activity during presentation of the word does seem to have some benefit, but even this effect is partly dependent on how the regions are defined. Older adults generally do not seem to show any effects of value in reward-sensitive regions overall, and individual differences in these effects tend not to correlate with recall performance. Interestingly, we do find that in older adults, value-related differences in activity in NAcc during the cue period correlate with effects of value on recollection estimates from the later recognition test. While this result is still somewhat tentative, it does support the idea that with a longer delay between study and test, effects of value in dopaminergic reward regions of the brain would have a stronger effect in a paradigm otherwise similar to ours. Young adults do not show a similar effect, but it may be that, due to slower forgetting rates in young adults, the delay period was not long enough for such an effect to emerge in young adults.

The results from Chapter 4 also suggest that dual-process methods may be a useful way to distinguish between effects of value that are mediated by selective application of effective encoding strategies, versus effects of value that are largely automatic and potentially dopamine-driven. Specifically, when people are given the opportunity to use metacognition to control strategy use, and claim to be sensitive to value, they tend to show effects of value on both recollection and familiarity. When such metacognitive opportunities are not available, or in individuals who claim to not be motivated to change encoding strategies as a function of value even when practice opportunities are available, high-value items are still more likely to be recollected, but familiarity is not affected by value. This distinction is consistent with what prior literature has generally shown, and while it would need to be validated via further studies, it seems to be a promising methodological advance for studying different ways by which encoding manipulations can affect memory.

Finally, the fMRI analyses presented in Chapter 4 produced a rich, though complicated, dataset. It is notable that the negative correlations between value-related differences in activity in posterior medial brain regions and effects of value on recollection in young adults were maintained when recalled items were excluded from the analysis, while the positive brain-behavior correlations in regions related to semantic processing were not. Those results suggest that increased deactivation of default-mode brain regions may be a separate but important mechanism of selective encoding, even if it was less effective than was selective semantic encoding at improving memory on an immediate free recall test. It is plausible that such mechanisms are responsible for the apparently automatic effects of value on recollection that are observed behaviorally in young adults when the appropriate task context to evoke selective strategy use is not provided, but further work would be necessary to support this speculation.

The analogous finding in older adults, a negative brain-behavior correlation with effects of value on familiarity in brain regions that are near to but not overlapping with those showing this effect in young adults, may or may not reflect a similar mechanism. The fact that older adults, but not young adults, show a brain-behavior correlation with familiarity, while at the same time older adults show a stronger behavioral effect of value on familiarity than do young adults, suggests that this deactivation does play an important role in selective encoding in older adults, specifically in whatever processes lead to greater familiarity on the later recognition test. These data also show an intriguing tradeoff in a number of brain regions, by which decreases in activation, or reduced increases in activation, as a function of value both increase beneficial effects of value on familiarity and decrease beneficial effects of value on recollection. As elaborated above, this finding supports an intriguing speculation that the same elaborative encoding mechanisms that enhance recollection also distract from the ability to encode items in a way that will lead to greater familiarity, and thus older adults may have to make a choice, based in part on their level of fatigue, of which mechanism to engage. Again, however, further work would be necessary to support this speculation.

Future directions

A number of promising directions for future work are apparent in this line of research. One such direction is to further explore the conditions under which proactive engagement of semantic processing regions and/or reward-sensitive regions enhance encoding and when they do not. It would then be possible to determine whether older adults show a deficit in such encoding tasks. If their success in the value-directed remembering task is just a “lucky” convergence between brain mechanisms that are effective for modulating the effectiveness of encoding in a particular task and mechanisms that are preserved with healthy aging, we might expect that older adults would be impaired in such a task, as has been shown previously by Bollinger et al. (2011). On the other hand, if they are being strategic at allocating encoding resources, they may be able to reallocate resources to selectively engage proactive encoding mechanisms under the appropriate conditions.

Another important future direction would be to further explore the distinction between the strategy-driven effects of value that are the main focus of most of this dissertation, and the more automatic effects that are apparent in the recognition tests that are the focus of Chapter 4. Those automatic effects may reflect deactivation of default-mode regions, they may represent activation of dopaminergic reward regions, or there could be some other mechanism involved. As described above, these automatic effects seem to lead to increases in recollection for non-recalled items in young adults, but, based on Experiment 1B, may instead lead to increases in familiarity in older adults. In any case, these effects deserve more careful examination. One possible way to do this would be to design an fMRI study of value-directed remembering that includes a plurals manipulation, or some other manipulation of source details, to the value-directed remembering paradigm, as we did in Experiments 4 and 5. Assuming that there would be enough trials for which item but not source memory is available, it would then be possible to separate the neural mechanisms by which value enhances familiarity from the mechanisms by which value enhances recollection.

Another useful implication would be to find ways in which the environment can be optimized to allow older adults to make more efficient use of their preserved cognitive resources. In Chapter 3, we noted that "to optimize the efficiency of memory performance in older adults, they should be given the opportunity to selectively and reactively engage semantic encoding processes for important information." In combination with the results reported in Chapter 4, it is possible to turn this into a more concrete recommendation: in order for older adults more easily learn important information, and potentially for them to learn any effortful task, it is particularly important to provide older adults with an opportunity for practice and feedback. Indeed, in any task in which it is important to learn to engage a particular type of strategy in order to perform well, it seems that providing practice and feedback could be an important way for people to use metacognition to improve their use of such strategies. Interestingly, practice is often thought of as being particularly useful for learning implicit tasks, such as riding a bicycle or playing the piano, so it is interesting that here, it seems to be necessary for the engagement of explicit strategies.

A final potential way to extend these findings would be to see how value affects encoding in a paradigm in which attempts to explicitly encode the study items are actually counterproductive. Such a paradigm has been developed in recent years, using abstract kaleidoscopes as stimuli, together with a forced choice recognition test. Under these conditions, memory is better under divided attention conditions than under full attention conditions, and tends to be better when people are less confident than when they are relatively more confident (Voss, Baym, & Paller, 2008). It would be intriguing to see whether people are able to adapt away from using explicit strategies under these conditions, or whether they would persist in trying to use explicit strategies to encode valuable items, even to their own detriment.

Appendix A
Tables of activity peaks for young adult fMRI data

Table A.1A. Activation peaks for regions showing value effects (High – Low) in young adults during value cue period. Coordinates are listed in Montreal Neurological Institute (MNI) space.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels in cluster
1	L lingual gyrus	17	5.10	-20	-96	-4	4645
	R lingual gyrus	17	4.85	22	-98	-4	
	L inferior occipital gyrus	18	4.46	-30	-88	-4	
	L fusiform gyrus	18/19	4.33	-22	-88	-18	
	R fusiform gyrus	18/19	3.99	28	-88	-10	
	R cuneus	18	3.62	24	-100	6	
	L cuneus	18	3.47	-20	-88	10	
	L cerebellum	--	3.14	-32	-76	-36	
	R inferior occipital gyrus	18	3.04	36	-80	-2	
	R cerebellum	--	3.03	30	-76	-20	
2	L middle frontal gyrus	9/46	3.88	-44	34	24	2966
	L premotor cortex	6	3.30	-38	0	60	
	L frontal pole	10	3.28	-30	54	8	
	L IFG pars opercularis	44	3.21	-46	20	8	
	L precentral gyrus	4	2.94	-50	2	22	
3	L supramarginal gyrus	40	4.35	-44	-48	52	1822
	L superior lateral occipital cortex	19	3.44	-32	-64	48	

	L angular gyrus	39	2.80	-36	-58	36	
	L superior parietal lobule	7	2.36	-24	-52	42	
4	R frontal pole	10	3.43	26	48	-4	1101
	L anterior cingulate	24	3.18	-8	38	2	
	R anterior cingulate/ paracingulate gyrus	24/32	3.17	4	44	24	
	L medial frontal gyrus	10	2.51	-2	54	-8	
5	R supramarginal gyrus	40	3.38	48	-40	42	1053
	R angular gyrus	39	3.23	38	-56	48	
	R superior parietal lobule	7	2.92	38	-46	44	
	R superior occipital gyrus	19	2.87	28	-64	54	
	R precentral gyrus	4	2.63	28	-18	50	
6	R nucleus accumbens	34	3.66	8	10	-6	1018
	L nucleus accumbens	34	3.49	-6	8	-4	
	R/L thalamus	--	3.28	2	-2	4	
	R caudate	--	2.86	10	16	6	
	L caudate	--	2.86	-10	16	2	
	L putamen	--	2.83	-14	6	-12	
	L pallidum	--	2.43	-16	-2	-6	
7	L inferior temporal gyrus	37	3.27	-52	-60	-16	433
	L cerebellum	--	2.87	-42	-62	-24	
	L fusiform gyrus	37	2.85	-36	-50	24	

	L inferior occipital gyrus	19	2.75	-50	-70	-16	
8	R middle temporal gyrus	21/37	3.34	58	-46	-8	411

Table A.1B. Activation peaks for regions showing reverse value effects (Low – High) in young adults during value cue period.

Cluster	**Peak**	**BA**	**z-stat**	**X**	**Y**	**Z**	**Voxels in cluster**
1	R superior occipital gyrus	19	-3.47	28	-86	40	664
	R cuneus	18	-3.40	2	-86	26	
2	L fusiform gyrus	19	-3.49	-24	-54	-12	427
	L lingual gyrus	19	-3.44	-14	-44	-8	

Table A.2A. Activation peaks for regions showing value effects (High – Low value) during word encoding period.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels in cluster
1	L supplementary motor area (SMA)	6	4.88	-8	8	62	24967
	L IFG pars triangularis	45	4.56	-44	32	6	
	L IFG pars opercularis	44/9	4.54	-42	8	18	
	R putamen	--	4.47	22	6	-8	
	L caudate	--	4.47	-16	10	10	
	L premotor cortex	6/8	4.42	-26	-2	54	
	L temporal pole	38	4.42	-54	10	-6	
	L precentral gyrus	4	4.38	-50	2	48	
	L supramarginal gyrus	40	4.35	-50	-42	28	
	L superior temporal gyrus	22	4.33	-50	-34	2	
	R superior frontal gyrus	8	4.32	2	14	56	
	L pallidum	--	4.30	-14	6	-4	
	L inferior temporal gyrus	19/37	4.29	-46	-52	-12	
	L paracingulate gyrus/anterior cingulate	32	4.28	-6	14	46	
	R SMA	6	4.22	6	4	64	
	L putamen	--	4.20	-24	8	0	
	L middle temporal gyrus	21	4.08	-46	-50	8	
	L thalamus	--	4.07	-8	-2	8	
	R premotor cortex	6	3.80	26	2	54	

	L angular gyrus	39	3.73	-58	-58	14	
	L superior occipital gyrus	19	3.61	-20	-66	52	
	L cerebellum	--	3.56	-48	-54	-30	
	L superior parietal lobule	7	3.51	-30	-42	42	
	L orbital frontal cortex	11	3.46	-40	34	-14	
	L superior frontal gyrus	8	3.44	-4	40	52	
	L middle frontal gyrus	46	3.38	-46	36	22	
	L medial frontal cortex	9	3.35	-8	58	34	
	L frontal pole	10	3.31	-34	46	18	
	L insula	13	3.25	-36	14	0	
	L inferior occipital gyrus	18	3.25	-46	-66	-2	
	R caudate	--	3.16	10	12	2	
	R precentral gyrus	4	3.14	28	-8	64	
	R thalamus	--	2.98	16	-18	8	
	R anterior cingulate	24	2.97	8	16	36	
	L midbrain	--	2.87	-8	-22	-14	
	R hippocampus	34	2.58	20	-14	-16	
	R amygdala	25	2.57	22	-2	-18	
2	R IFG pars opercularis	44	3.81	50	18	16	2748
	R IFG pars orbitalis	45/47	3.79	56	36	0	
	R precentral gyrus	4	3.69	52	-10	40	
	R supramarginal gyrus	40	3.31	40	-30	36	
	R postcentral gyrus	3	3.28	56	-6	16	

	R temporal pole	38	3.23	54	16	-8	
3	R superior/middle temporal gyrus	22	4.37	52	-28	0	904
	R superior temporal gyrus	42	3.59	66	-36	18	
4	L inferior occipital gyrus	18	3.79	-36	-90	-2	844
	L lingual gyrus	17	3.54	-18	-96	-6	
5	R cerebellum	--	4.12	34	-62	-26	591
6	R lingual gyrus	17/18	4.33	26	-94	-4	472
	R inferior occipital gyrus	18	2.87	42	-86	-8	

Table A.2B. Activation peaks for regions showing reverse value effects (Low – High value) during word encoding period.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels in cluster
1	L cuneus	19	-4.14	-6	-82	40	3777
	L precuneus	7	-4.09	-2	-72	26	
	R cuneus	18/19	-3.89	4	-82	38	
	R superior occipital gyrus	18	-3.50	26	-88	22	
	R precuneus	7	-3.30	18	-60	30	
	L superior occipital gyrus	19	-3.33	-14	-90	38	
2	R angular gyrus	39	-3.50	58	-48	30	671
	R supramarginal gyrus	40	-3.08	56	-40	36	
3	R superior posterior cingulate	31	-3.44	2	-38	40	609
	L inferior posterior cingulate	23	-3.33	-2	-40	24	
	R precuneus	31	-2.82	6	-38	50	

Table A.3. Activation peaks for regions showing significant correlations between selectivity index and value effects (High > Low contrast) during word encoding period.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels
1	L superior frontal gyrus	8	4.13	-4	26	52	1612
	L paracingulate gyrus	32	3.97	-2	34	38	
	L supplementary motor area (SMA)	6	3.78	-4	14	64	
	L premotor cortex	6	3.60	-28	10	58	
	R SMA	6	3.26	6	12	60	
2	L IFG pars orbitalis	47	4.02	-46	20	-6	1397
	L middle frontal gyrus	46	3.80	-50	40	10	
	L IFG pars triangularis	45	3.76	-46	22	16	
	L IFG pars opercularis	44	3.75	-54	12	-2	
	L frontal pole	10	3.73	-40	42	-10	
	L precentral gyrus	4	3.24	-48	6	10	
	L insula	13	2.92	-40	2	0	
3	L putamen	--	3.7	-20	4	-4	562
	L insula	13	3.54	-30	20	-6	
	L caudate	--	3.23	-12	12	8	
4	L inferior occipital/ posterior middle temporal gyrus	19	3.5	-52	-64	-2	457
	L inferior temporal gyrus	37	3.49	-48	-56	-14	
	L middle temporal gyrus	21	3.36	-60	-56	-4	
	L fusiform gyrus	37	3.17	-34	-42	-14	

5	L precentral gyrus	4	3.86	-38	6	28	388
	L IFG pars opercularis	44	3.77	-48	8	28	
	L premotor cortex	6	3.76	-42	8	38	

Appendix B

Tables of activity peaks for older adult fMRI data, and for comparisons across age groups

Table B.1A. Activation peaks for regions showing a significant difference in brain activity for High – Low value items during the word-encoding period in older adults.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels
1	L inferior occipital gyrus	18/19	5.31	-32	-100	0	4116
	R inferior occipital gyrus	17/18	4.68	32	-96	-8	
	R cerebellum (posterior)	--	4.08	36	-76	-24	
	L fusiform gyrus	19/37	3.92	-22	-90	-14	
	R cerebellum (anterior)	--	3.58	32	-56	-32	
	R middle occipital gyrus	18	3.53	38	-86	2	
	L lingual gyrus	17/18	3.35	-10	-104	-6	
	L middle temporal gyrus	37	3.34	-60	-52	-4	
	L cerebellum (posterior)	--	3.33	-44	-70	-26	
	L inferior temporal gyrus	20	3.28	-58	-58	-14	
2	L superior frontal gyrus (pre-SMA)	6	4.13	-2	10	66	3729
	L middle frontal gyrus (dorsolateral PFC)	9	4.05	-52	20	28	
	L inferior frontal gyrus, pars opercularis	44	3.84	-50	8	12	
	L inferior frontal gyrus, pars triangularis	45	3.58	-44	28	18	
	L inferior frontal gyrus, pars orbitalis	47	3.56	-44	38	6	
	L temporal pole	38	3.56	-52	20	-10	

	L orbitofrontal cortex	11	3.32	-42	26	-16	
	L medial frontal gyrus	6	3.21	-6	4	52	
3	L superior lateral occipital	19	3.59	-24	-72	50	1497
	L precuneus	7	3.40	-12	-74	58	
	L supramarginal gyrus	40	3.28	-48	-42	56	
	L superior parietal lobule	7	3.07	-38	-46	48	

Table B.1B. Activation peaks for regions showing a significant difference in brain activity for Low - High value items during the word-encoding period in older adults.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels
1	R angular gyrus	39	3.51	56	-54	34	617
	R supramarginal gyrus	40	3.39	62	-40	32	

Table B.2A. Activation peaks for regions in which the difference in brain activity for High – Low value items is greater for young adults than older adults during the word-encoding period, masked by voxels showing a positive effect of value in either young or older adults.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels
1	L putamen	--	3.44	-22	0	6	1271
	L inferior frontal gyrus, pars opercularis	44	3.23	-58	18	-2	
	L inferior frontal gyrus, pars orbitalis	47	3.06	-38	28	-4	
	L inferior frontal gyrus, pars triangularis	45	3.01	-46	32	6	
	L caudate	--	2.99	-10	14	10	
	L insula	13	2.80	-36	4	0	
2	L superior frontal gyrus	6	3.87	-4	24	60	742
	R superior frontal gyrus	6	3.33	8	10	62	
	L paracingulate gyrus	32	2.93	-4	14	48	
	R supplementary motor area	6	2.73	2	-4	66	
3	L supramarginal gyrus	40	3.77	-46	-44	10	538
	L superior temporal gyrus	22	3.23	-50	-36	4	
	L middle temporal gyrus	22	2.96	-54	-46	4	
4	R putamen	--	3.60	22	8	-6	375
5	L middle frontal gyrus	6	3.25	-48	4	50	274
	L precentral gyrus	4	3.07	-50	-6	44	
6	L inferior frontal gyrus, pars opercularis	44	3.25	-42	14	20	256

Table B.2B. Activation peaks for regions in which the difference in brain activity for Low - High value items is greater for young adults than older adults during the word-encoding period, masked by voxels showing a negative effect of value in either young or older adults.

Cluster	**Peak**	**BA**	**z-stat**	**X**	**Y**	**Z**	**Voxels**
1	L/R precuneus	7/31	3.46	-4	-76	46	928
	R cuneus	18	3.33	2	-82	26	
	L cuneus	19	3.09	-6	-86	36	
	L posterior cingulate	31	3.08	-18	-64	22	

Table B.3. Activation peaks for regions in which High – Low difference in brain activity during the word-encoding period correlates with selectivity index for older adults.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels
1	L inferior frontal gyrus, pars opercularis	44	3.67	-48	12	28	1445
	L precentral gyrus	6	3.41	-44	-2	54	
	L middle/superior frontal gyrus	6	3.04	-30	16	56	
	L inferior frontal gryus, pars triangularis	45	3.00	-48	28	22	
	L middle frontal gyrus	9	2.56	-52	22	32	
2	R cerebellum (posterior)	--	3.54	32	-70	30	397
3	L lingual gyrus	17	4.22	-14	-108	-8	381
	L inferior occipital gyrus	18	3.57	-36	-96	-6	
	L fusiform gyrus	19	3.04	-26	-86	-14	
4	R lingual gyrus	17/18	5.06	24	-102	0	376
	R inferior occipital gyrus	18	3.35	28	-88	-4	
5	L middle/inferior temporal gyrus	37	3.62	-60	-56	-8	363
	L inferior occipital gyrus	19	3.33	-56	-68	-2	
6	L medial frontal gyrus (supplementary motor area)	6	3.26	-4	2	56	312
	L paracingulate gyrus	32	3.03	-2	12	46	
	L superior frontal gyrus	6	2.92	0	12	56	

Table B.4. Activation peaks for regions in which Young > Old for the correlation between the High – Low value difference in activity and selectivity index, masked by voxels showing this effect in either young or older adults.

Cluster	**Peak**	**BA**	**z-stat**	**X**	**Y**	**Z**	**Voxels**
1	L superior frontal gyrus	6	3.43	-2	22	58	388
2	L inferior frontal gyrus, pars triangularis	45/47	3.44	-50	26	-4	162
	L inferior frontal gyrus, pars opercularis	44	3.27	-52	14	-2	

Table B.5. Activation peaks for regions in which the difference in brain activity for High – Low value items is greater for young adults than older adults during the cue period, masked by voxels showing this effect in either young or older adults.

Cluster	Peak	BA	z-stat	X	Y	Z	Voxels
1	L middle frontal gyrus	9/46	3.96	-42	34	24	463
	L precentral gyrus	6	3.07	-48	2	22	
	L inferior frontal gyrus, pars opercularis	44	3.00	-46	20	24	
	L frontal pole	10	2.92	-42	44	20	
2	L supramarginal gyrus/ angular gyrus	40/39	3.42	-50	-42	46	447
	L superior parietal lobule	7	3.27	-42	-48	52	
3	L cuneus	18	3.81	-20	-96	16	326
	L lingual gyrus	17/18	3.56	-6	-100	2	
4	L frontal pole	10	3.28	-28	52	8	254
5	R anterior cingulate	32	3.06	20	42	0	192
	R frontal pole	10	2.96	42	40	2	

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