

Cognitive and Neural Correlates of Implicit Associative Memory in Young and Older Adults

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## ABSTRACT

ILANA T. Z. DEW: Cognitive and Neural Correlates of Implicit Associative Memory in  
Young and Older Adults

(Under the direction of Kelly S. Giovanello)

Declines in episodic memory are a hallmark of cognitive aging. One explanation is an age-related deficit in binding, or associating, the separate contextual features of a memory event, a process that depends on the medial temporal lobes (MTL). An alternative viewpoint links the episodic memory declines to an impairment in strategic recollection of contextual features, a process that depends more on the prefrontal cortex (PFC). Assessing implicit memory of new associations is a way to distinguish between these viewpoints. To date, mixed findings have emerged from studies of implicit associative memory in aging. One factor that may account for the variability is whether the manipulations inadvertently involve explicit processes. In 6 experiments I present a novel paradigm of conceptual associative priming in which subjects make speeded associative judgments about unrelated objects. Using a size classification task, Experiment 1 showed equivalent associative priming between young and older adults. Experiment 2 generalized the results of Experiment 1 to an inside/outside classification task, while replicating the typical age-related impairment in associative recognition. Experiment 3 showed that associative priming in this task cannot be explained by explicit contamination. In Experiments 4 and 5, older adults showed preserved rapid response learning, a complementary form of incidental associative processing. Lastly, Experiment 6 used event-related fMRI to examine the neural basis of associative priming. During implicit associative retrieval, older adults showed under-recruitment of MTL regions coupled with over-recruitment of right dorsolateral PFC. Furthermore, activity in right

dorsolateral prefrontal cortex correlated with behavioral priming in older but not young adults, consistent with the hypothesis that older adults may recruit prefrontal regions to compensate for MTL dysfunction. This study documents the first evidence that recruitment of right DLPFC operates during associative priming, on a task in which no age differences were found behaviorally. Taken together, the experiments provide an important example of a form of associative processing that is unimpaired in older adults. However, an absence of age differences in the behavioral measure did not map onto the same pattern of neural activations in the two age groups. This finding is consistent with patterns of structure-function reorganization in aging.

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## CHAPTER I.

### INTRODUCTION

Older adults do not perform as well as younger adults on tests of episodic memory (for a review, see Hoyer & Verhaeghen, 2006). Episodic memories are contextually-specific, such as an event that occurred at a particular place and at a particular time (Tulving, 1983). Age differences have been found in memory for a range of contextual attributes, such as temporal order (Cabeza, Anderson, Houle, Mangels & Nyberg, 2000; Fabiani & Friedman, 1997), location (Glisky, Rubin & Davidson, 2001), the source of a new piece of information (Johnson, Hashtroudi & Lindsay, 1993) and perceptual characteristics such as voice (Naveh-Benjamin & Craik, 1996; Bayen & Murnane, 1996; Pilotti, Meade & Gallo, 2003). Age-related deficits have been found to be substantially larger for contextual details than for content items (Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995).

The exact mechanism that gives rise to this context memory impairment remains uncertain. One explanation is an age-related impairment in the *process of binding* together the separate elements of a to-be-remembered episode (Chalfonte & Johnson, 1996; Lyle, Bloise, & Johnson, 2006; Mitchell, Johnson, Raye & D'Esposito, 2000). Across different paradigms, this process has been described in different ways: as an impairment in feature binding (Chalfonte & Johnson, 1996; Mitchell, Johnson, Raye & D'Esposito, 2000), as a difficulty in creating an ensemble of item and context (Bayen, Phelps, & Spaniol, 2000), or as deficits in semantic, featural, or temporal relational memory (Cabeza, 2006). The hypothesis that a deficit in the creation and retrieval of links among individual units of

information can account for the observed episodic memory impairments has been formalized as the Associative Deficit Hypothesis (ADH) (Naveh-Benjamin, 2000). Indeed, relative to memory for single items, older adults have shown poorer memory than young adults for multiple types of associations, including picture-location (Chalfonte & Johnson, 1996), picture-color (Chalfonte & Johnson, 1996), word-font (Naveh-Benjamin, 2000), word-word (Naveh-Benjamin, 2000), word-nonword (Naveh-Benjamin, 2000), picture-picture (Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003), face-name (Naveh-Benjamin, Guez, Kilb & Reedy 2004), face-spatial location (Bastin & Van der Linden, 2006) and face-face (Bastin & Van der Linden, 2006) associations. Research in neuropsychology and cognitive neuroscience indicates that the medial temporal lobe, and in particular the hippocampus, serves this function of binding elements together into a learning event, and operates both incidentally and obligatorily (e.g., Eichenbaum, Yonelinas & Ranganath, 2007; Moscovitch, 1992).

An alternative viewpoint accounts for impairments in episodic or associative memory as a part of a more generalized decline in strategic, consciously-controlled process. Such processes include the intentional manipulation, organization, or evaluation of features and, especially, the conscious, intentional retrieval of items within their studied context (i.e., item-context associations), a process that is often referred to as *recollection*. According to this view, impairments will be less evident on tests that require automatic or unintentional memory processes, such as familiarity-based recognition (Anderson & Craik, 2000; Hudson, 2008; Jacoby, 1999; Jennings & Jacoby, 1993; Light, Prull, LaVoie & Healy, 2000; Naveh-Benjamin, Shing, Kilb, Werkle-Bergner, & Lindenberger, 2009; Moscovitch & Winocur, 1995). This viewpoint coincides with other, more general, frameworks of cognitive aging

that posit deficits in self-initiated processes (Craik, 1986; Smith, Park, Earles, Shaw & Whiting, 1998), encoding strategy (Dunlosky & Hertzog, 1998; Kausler, 1994), or processing resources (Craik & Byrd, 1982). These consciously-controlled mechanisms operate under effortful, intentional conditions, and have been linked to the prefrontal cortex (PFC) (Buckner, 2003).

Considerable evidence exists for both a binding deficit (e.g., Naveh-Benjamin, 2000), as well as a recollection deficit (e.g., Jacoby, 1999; Naveh-Benjamin et al., 2009) in aging. Indeed, associative-binding processes and strategic associative retrieval processes are known to work together to support the encoding and retrieval of episodic memories. However, these viewpoints do make competing predictions in two critical ways: First, although the ADH emphasizes a deficit in the encoding and retrieval of associative information, the recollection deficit view emphasizes an impairment at the retrieval stage (see Naveh-Benjamin & Old, 2008, for a recent discussion). Second: the hypotheses of a binding deficit and a recollection deficit offer different predictions about the status of implicit memory.

Implicit memory refers to non-conscious, unintentional influences of memory, and is measured through priming -- when some aspect of a previous experience influences or facilitates behavior in a new, seemingly unrelated situation (Roediger, 1990; Schacter, 1987). Unlike explicit tests such as recall or recognition, implicit test instructions typically make no mention of the study episode. Although strong empirical support exists for an age-related deficit in associative memory, the interpretation may be confounded by the fact that the majority of studies examine only direct, explicit tests of new associations. Less is known about the status of implicit associative memory in aging. Importantly, a deficit in strategic recollection of associative information accommodates the possibility that unintentional, or

non-consciously controlled processes may be relatively unimpaired by aging, even if they involve associative information. In contrast, binding is characterized as an incidental, obligatory process that operates independently from conscious intent (Moscovitch, 1992). As such, if a deficit in binding mechanisms at encoding can explain later episodic memory impairment, then such a deficit should be evident using tests of both explicit and implicit retrieval. Alternatively, if older adults are impaired in strategic, controlled processing of relational information, then an age-related deficit should not occur with implicit testing.

Although, theoretically, the implicit memory approach provides a promising method with which to help clarify the age deficit in context memory, research taking this approach has provided mixed evidence. Tests that have been used to assess associative priming have varied according to type of association, stimulus materials, level of environmental support, and dependent measures; as such, few definitive patterns have yet emerged. The present dissertation reviews how implicit memory for new associations has been shown to operate in aging, merging evidence from behavioral priming paradigms, neuropsychology, and cognitive neuroscience. Building on the prior findings, the results and analyses of six experiments are then described.

## CHAPTER II.

### TESTING ASSOCIATIVE MEMORY

The typical paradigm used to examine both explicit and implicit associative memory involves first a study portion, in which subjects encode novel associations in any of various ways; depending on study goals. After a brief distractor period in which they are engaged in an unrelated cognitive task, subjects complete the test portion of the experiment. At a general level, explicit and implicit tests are differentiated by whether or not the subjects are instructed to think back to the earlier items in order to complete the task.

Novel associations may be characterized as *inter-item* (i.e., between two independent items), or *intra-item* (i.e., between an item and a concrete, stimulus-bound contextual feature, such as color, font, or perceptual modality). Although across some papers there are subtle variations in the details of the task, explicit memory for inter-item pairs is typically tested using an associative recognition paradigm, originally used by Humphreys (1976). In the standard version of this test, subjects study unrelated pairs (e.g., between two unrelated words, or between an item and a concrete feature of that item). At test, some item-item or item-feature pairs are presented that were encoded together at study (*intact*), some pairs are presented in which both units were studied but not together (*recombined*), and some pairs consist of two new, unstudied units. Participants are asked to decide whether the presented pair was seen together previously. Associative recognition accuracy is calculated as the difference between hit rate for intact pairs and the false alarm rate to recombined pairs. If participants encode both elements individually, but have difficulty integrating them together



into a cohesive unit, then hit rates to intact pairs will be high but recombined pairs will elicit false alarms, and in turn decreasing accuracy.

Explicit memory for intra-item associations is tested similarly. For example, participants may study a list of words, each presented in one of several fonts. At test, some studied words are presented in the same font as at study, some studied words are presented in a different studied font, and the remaining items are new, unstudied words presented in new, unstudied fonts. Associative recognition accuracy is measured with the same procedures as for inter-item associations.

Unlike explicit tests, which instruct subjects to think back to the study episode, implicit memory is measured by facilitated task performance for repeated stimuli relative to new stimuli, independent from conscious, intentional retrieval processes (Mulligan, 2003; Roediger, 1990; Schacter, 1987). Initially, implicit memory for new associations was not thought possible. Establishing novel connections was thought to necessitate elaborative processes, supported only by conscious retrieval (e.g., Cermak, Bleich, & Blackford, 1988), and priming of any kind was thought to depend on pre-existing representations. More recently, priming of novel associations (sometimes called episodic priming, see McKoon & Ratcliff, 1979) has been demonstrated in numerous studies.

Priming of new associations is typically measured as facilitated task performance for items that are presented in the same context as at study, relative to a different context. One common implicit test for inter-item associations is associative word-stem completion (WSC). At study, subjects encode pairs of unrelated items (e.g., window-reason). At test, the first item of a pair is presented, followed by the first few letters of a second word. Participants are instructed to complete the stem with the first word that comes to mind after having read the

first word. Associative priming is demonstrated if subjects are more likely to complete the stem with the studied word when the stem is presented in the same context as at study (e.g., window – rea\_\_\_\_\_) relative to a different context (e.g., hammer – rea\_\_\_\_). Another common example is speeded reading, in which participants indicate via key press as soon as they have read two words (either alone or embedded within a sentence). Here, associative priming is demonstrated if subjects are faster to read previously paired words or sentences relative to recombined.

Priming of intra-item associations is often tested using the same paradigms that assess repetition priming of single items. Associative priming is found on these tasks if a change in a surface-level feature of the item reduces the magnitude of repetition priming. The perceptual identification task is one example, in which words are presented very briefly, and participants are instructed to try to identify the presented word. On this task, repetition (item) priming is evident if earlier target words are easier to identify than counterbalanced new words. Sensitivity to a surface-level alteration (e.g., changing its font or perceptual modality from study to test) can be seen as evidence of initial success in binding the item with its concrete features. The benefit in priming for items that retain their initial surface form is sometimes called feature-specific or form-specific priming; this priming benefit is often attributed to the degree of perceptual overlap between study and test (Roediger & Blaxton, 1987).

## CHAPTER III.

### EFFECTS OF AGING ON IMPLICIT MEMORY FOR NEW ASSOCIATIONS

To date, studies of implicit associative memory in aging have produced mixed findings. As described previously, priming of new associations is measured as facilitated task performance for items that are presented in the same context as at study, relative to a different context. The item-context relationships are sometimes operationalized as an item and a concrete feature of that item, such as its color or font (*intra-item* associations) and sometimes operationalized as two unrelated items that are presented together (*inter-item* associations). Intra-item associations, such as those between an item and its color, require the integration of an item and its surface-level features; on these perceptual manipulations, older adults typically show priming to the same extent as younger adults (Gibson, Brooks, Friedman & Yesavage, 1993; Light, LaVoie, Valencia-Laver Albertson-Owens & Mead, 1992; Lloyd-Jones, 2005; Wiggs & Martin, 1994;). Age equivalence is also found on inter-item associations if perceptually-driven integration occurs between shallow, surface-level features of the items (Light, Kennison, Prull, LaVoie & Zuellig, 1996; Monti et al., 1997). Findings from these perceptually-based paradigms have suggested that there is no age difference in implicit associative memory.

However, when tasks require the meaningful integration of unrelated items, older adults have shown lower, or even no evidence of, associative priming (Ergis, Van der Linden, & Deweer, 1998; Howard, Fry, & Brune, 1991; Howard, Heisey & Shaw, 1986; Monti et al., 1997; O'Hanlon, Wilcox & Kemper, 2001; Spieler & Balota, 1996), An

exception is if environmental support or special encoding conditions are implemented in order to improve older adults' performance (Howard, et al., 1991; Howard, et al., 1986). Such exceptions are consistent with the explicit memory literature, which has shown that older adults are less likely than young adults to process relational information spontaneously, but improve their performance when provided with a specific strategy for associative encoding and retrieval (Naveh-Benjamin, Brav & Levy, 2007; Old & Naveh-Benjamin, 2008).

The differential age effect for priming of intra- versus inter-item associations are described in more detail below.

## CHAPTER IV.

### INTRA-ITEM ASSOCIATIVE PRIMING

Age differences are not typically found on priming for intra-item (i.e., item-feature) associations. An early demonstration of this (Light, LaVoie, Valencia-Laver, Albertson-Owens, & Mead, 1992) compared explicit and implicit memory for perceptual modality. After reading or listening to a series of words, participants completed an explicit test for each item's initial perceptual modality. Participants also completed one of two implicit tests: a visual perceptual identification test in which participants were instructed to identify briefly presented words, or an auditory version of the same test, in which participants were instructed to identify words that were masked in noise. Context effects were measured by comparing within-modal and cross-modal magnitudes of priming. On the explicit measure, as expected, the younger adults were significantly better at remembering context information. On the implicit measure, results demonstrated equal modality effects for young and older adults. The identification of words presented in both the within-modal and the cross-modal conditions was greater than the identification of new words, and the difference between within-modal and cross-modal priming was equal across the age groups. This sensitivity to modality change provided evidence that the items were bound with their initial perceptual mode despite impairments on the explicit measure. Similar modality effects have been replicated in multiple priming studies (e.g., in Pilotti & Beyer, 2002), even though age effects are typically found on explicit tests of the same perceptual attribute (e.g., Kausler & Puckett, 1981).

Age invariance has also been demonstrated on priming for typeface font changes. In one example, young and older adults completed a syllable judgment task on words and were later tested on word-stem completion. Changing font reduced but did not eliminate priming for both age groups (Gibson, Brooks, Friedman, and Yesavage, 1993). A similar result has been found using speeded reading rather than WSC, in which both age groups were faster to read familiar English words when they were presented in their initial font relative to a changed font (Wiggs & Martin, 1994).

Taken together, the described studies provide evidence of unimpaired intra-associative priming for multiple types of contextual attributes, generalized across different implicit tests. One contrary example to this pattern is from Pilotti, Meade and Gallo (2003), who found that older adults were insensitive to a change in perceptual modality on an auditory perceptual identification task. However, the age effect was eliminated when controlling for differences in hearing acuity, suggesting that the finding was indicative of sensory-perceptual processing impairment. Similarly, some mixed evidence has emerged for effects of highly specific, fine-grained perceptual detail such as fundamental frequency. Older adults have in some studies shown equivalent sensitivity as young adults to study-to-test changes (e.g., Sommers, 1999); other studies have shown a priming reduction only in the young adults (Pilotti & Beyer, 2002; Schacter, Church & Osowiecki, 1994). However, across multiple types of cognitive tasks, older adults sometimes demonstrate difficulty in using sensory-perceptual information; this impairment may make unique contributions to tasks that involve these kinds of processes and that are otherwise unrelated to memory (Hashtroudi, Chrosniak & Schwartz, 1991; Hashtroudi, Johnson & Chrosniak, 1990). In turn, it is possible that a reduced sensitivity to these fine-grained perceptual details reflects a deficit in

organizing sensory-perceptual information rather than a deficit in memory for contextual detail.

## CHAPTER V.

### INTER-ITEM ASSOCIATIVE PRIMING

In contrast to the unimpaired priming of intra-item associations in aging, priming of new inter-item associations is typically reduced or not demonstrated at all in older adults. In one example (Howard, Heisey, and Shaw, 1986), participants studied sentences that meaningfully paired two unrelated nouns, and implicit memory was measured as a reaction time difference to recognize an item after it was preceded by the same or a different noun as at study. Younger but not older adults showed a reaction time difference to the context change, demonstrating impaired associative priming in the older adults. A similar result has been found across multiple studies that have used associative word stem completion (WSC), in which subjects are asked to complete a three-letter stem with the first word that comes to mind after reading the preceding word. After reading or creating sentences that integrate two unrelated words, younger adults have been repeatedly shown to be more likely than older adults to complete the stems in same-context relative to different-context presentations (Ergis, Van der Linden & Deweer, 1998; Howard, Fry, and Brune, 1991; O'Hanlon, Wilcox & Kemper, 2001).

This pattern of impaired inter-associative priming has been further generalized to a speeded naming task (Spieler & Balota, 1996). Younger and older participants were instructed to read a (prime) word silently, and then to read a (subsequent target) word out loud as quickly and accurately as possible. Response time was recorded as a function of prime repetition, target repetition, and prime-target pairing repetitions across trials. For the



younger adults, reaction time decreased more for pairing repetition relative to prime or target repetition alone. For the older adults, reaction time decreased to an equal extent as a function of target repetition and pairing repetition, demonstrating item but not associative priming.

There have been very few manipulations in which inter-item priming has been demonstrated in older adults to the same extent as younger adults. Critically, the ones that have shown this can be explained by two specifically relevant variables. The first condition under which no age difference is found is if inter-item associations are based on the integration of shallow, perceptually-driven features of the items. The second condition under which no age difference is found is when environmental support or special encoding conditions are implemented in order to improve older adults' performance.

An example of perceptually-driven inter-item associative priming comes from Light, Kennison, Prull, LaVoie, and Zuellig (1996), who found a similar magnitude of associative priming for nonwords in younger and older adults under single-trial study conditions. Participants read a series of two-syllable nonwords (e.g., kensess, patein) and were later measured on naming latency of nonwords, in which the component syllables were intact (e.g., kensess), recombined (e.g., kentein), or new. Older adults showed a similar benefit in naming speed for intact relative to recombined syllable combinations, despite predicted age effects on associative recognition. Because nonwords do not lend themselves to conceptual analysis, it is likely that participants relied on perceptual integration in order to form and facilitate later performance for these associations.

Perceptually-driven sources of priming have also produced age equivalence on a text rereading task. To examine perceptual sources of inter-item priming, Monti et al. (1997) compared text rereading speed when a globally meaningless sentence was repeated (e.g.

reading *that a fades Mountain and before*, at both trials) relative to when the words but not the between-word associations were repeated (e.g., *that a fades Mountain and before* at trial one and *Mountain a that before and fades* at trial two). Text rereading was equivalently faster for the intact sentences relative to recombined sentences for both young and older age groups.

As stated earlier, the second critical manipulation under which older adults have demonstrated unimpaired priming of inter-item associations is when environmental support is provided such that the encoding conditions are specially optimized. Examples of such support include providing specific strategies, multiple stimulus repetitions, or additional time to encode the pairs. (Indeed, providing older adults effective strategies has been shown to minimize the age differences even on explicit tests; see Dunlosky & Hertzog, 1998; Naveh-Benjamin, Brav & Levy, 2007). One example comes from Howard, Heisey, and Shaw (1986): Participants studied sentences that paired two unrelated nouns, and implicit memory was measured as a reaction time difference to recognize an item after it was presented in the same or a different context. Older adults demonstrated impaired priming under the sub-optimal encoding condition described earlier, in which sentences were presented only once, but not when the word pairs were presented multiple times at study. Similarly, Howard, Fry, and Brune (1991) found that when participants were given sentences at study and were later tested on associative word stem completion, younger but not older adults demonstrated priming. However, when older adults created their own sentences and time at study was self-paced, priming was comparable to that of younger adults. In both these studies, implicit associative memory could be supported in older adults under more favorable encoding conditions.

## CHAPTER VI.

### PERCEPTUAL-CONCEPTUAL VERSUS AUTOMATIC-CONTROLLED

Taken together, the pattern of preserved intra-item associative priming coupled with impaired inter-item associative priming implies a differential age effect for perceptually- and conceptually-based associative priming. This perceptual-conceptual distinction is critical in the examination of associative priming. According to principles of transfer-appropriate processing (TAP) (Morris, Bransford & Franks, 1977), memory performance will benefit to the extent that the cognitive operations required at study are reengaged at test. Implicit memory performance in particular has been sometimes attributed to the reengagement of perceptual or conceptual processing (for a review, see Roediger & McDermott, 1993). On tests that require primarily perceptual (i.e., data-driven) processing, such as the identification of perceptually-degraded stimuli, performance will benefit from similar perceptual analysis at study, and will show little sensitivity to conceptual analysis such as levels of processing or generation manipulations (Jacoby & Dallas, 1981; Jacoby, 1983; Roediger, 1990). Conversely, tests that are dependent on conceptual analysis benefit from similar conceptual processing at encoding, and show little or no sensitivity to alterations in orthographic or perceptual form (Bowers & Turner, 2003; Thompson-Schill & Gabrieli, 1999; Vaidya, Gabrieli, Verfaellie, Fleischman, & Askari, 1998). Like the priming of single items, research suggests that associative priming can also involve either – or both – perceptual or conceptual processes; the relative emphasis on one or the other depends on the items, the integration between them, and the retrieval task. If an associative implicit test emphasizes low-level

perceptual features, then perceptual components of the association will be recapitulated; if the test emphasizes meaningful features, then the conceptual components of the association will drive the priming effect. Reingold and Goshen-Gottstein (1996) showed that when the associative implicit test was a (conceptually-driven) relatedness judgment task, priming was not attenuated by cross-modal presentation for unrelated pairs. In contrast, a modality effect emerged on a perceptually-driven speeded lexical decision task.

However, what may be masked in the comparisons of perceptual and conceptual processing in aging is the more general framework of impaired strategic processes in aging relative to spared automatic memory processes. When the formation of associations occurs via the semantic integration of distinct items, associative priming has been shown to be sensitive to encoding manipulations that affect explicit retrieval processes, such as levels-of-processing manipulations (e.g., Graf & Schacter, 1985; O'Hanlon, Wilcox & Kemper, 2001; Reingold & Goshen-Gottstein, 1996). Conversely, when associations occur via the integration of perceptual features, associative priming has been shown to be sensitive to encoding manipulations that affect perceptual item priming, such as surface-feature changes (e.g., Gabrieli, Keane, Zarella, & Poldrack, 1997; Micco & Masson, 1991; Musen & O'Neill, 1997).

For instance, although associative word stem completion (WSC) is described as an implicit test (because it does not instruct subjects to think back to the studied items), it does not typically function as would a test that requires automatic, unintentional retrieval processes. Unlike the single item version of word stem completion, which been shown both to produce priming without intention or test-awareness (i.e., without noticing a connection between the items presented at study and during implicit testing), and which functions

independently from effortful processing (Roediger, 1990; for a recent example, see Dew & Mulligan, 2008), the associative version has instead been sensitive to the same variables that affect explicit retrieval processes. One example is from Bowers and Schacter (1990), who found that significant priming on associative WSC only occurred for participants who indicated test-awareness on a post-test questionnaire. Convergent evidence comes from neuropsychological studies of amnesic patients, which have shown that performance on the associative stem-completion task correlates positively with performance on explicit memory tests (e.g., Shimamura & Squire, 1989). Another example is from Kinoshita (1999), who found that following an elaborative encoding manipulation, divided attention at test affected associative word stem completion, but not item word stem completion. This same variable had no effect on a perceptual-associative inter-item implicit test: Light et al. (1996) showed that the speeded naming measure of compound nonwords (which showed age invariance) was unaffected by divided attention, despite decrements on associative recognition.

Complementary evidence for this pattern comes from a levels-of-processing manipulation on associative WSC. O'Hanlon, Wilcox, and Kemper (2001) compared older and younger adults on word stem completion for items, word stem completion for pairs, and cued recall, following syllable counting or sentence creation. Syllable counting did not benefit performance on paired associates cued recall or associative WSC for either age group. Sentence creation benefited young adults on both the associative priming and cued recall measure, though it only benefited older adults on cued recall and to a lesser extent than the young adults. Similar levels-of-processing effects on associative WSC and cued recall in the young adults support a functional connection between the tasks.

Given the typical use of strategic, elaborative encoding conditions, it is not surprising

that conceptually-driven inter-item associations have been particularly difficult to dissociate empirically from explicit memory (see McKone & Slee, 1997). Critically, if explicit retrieval strategies could be used to enhance performance on a nominally implicit test, it is likely that such strategies would be used more often and more successfully by younger adults (Habib, Jellicic & Craik, 1996). Thus, a difference in explicit contamination may be partly responsible for age differences. Furthermore, while explicit contamination could impact age differences during retrieval, strategic, consciously controlled processes could impact the age effect during encoding as well. Studies examining inter-item associations typically encourage the associative encoding of two unrelated words via semantic elaboration (e.g., creating a meaningful sentence that relates them). This kind of strategic encoding often benefits younger adults to a greater extent than older adults (Stuart, et al., 2006).

For these reasons, despite the theoretical usefulness of the implicit memory approach, it is unclear whether prior tasks of conceptual associative priming have validly reflected implicit memory. In turn, the age effects to date are difficult to interpret. Experiments 1 and 2 in this dissertation test whether older adults can show implicit memory for new conceptual associations, using a novel speeded response paradigm that was designed to be more likely than prior associative priming paradigms to tap unintentional, non-conscious response mechanisms. Experiment 3 tests the validity of this assumption by determining whether associative priming using this paradigm can be dissociated from explicit memory. If older adults have a deficit in binding mechanisms that affects not only strategic, intentional associative encoding and retrieval but also incidental associative processing, then they should show impaired conceptual associative priming relative to young adults, as has been found in prior studies. If, however, older adults can encode meaningful associations incidentally but

have difficulty with strategic or evaluative associative memory processes, then no difference in priming should emerge between the age groups using this new paradigm.

## CHAPTER VII.

### RAPID RESPONSE LEARNING: IMPLICATIONS FOR ASSOCIATIVE MEMORY DECLINE IN AGING

As described, implicit memory is a nonconscious, unintentional form of memory retrieval, and is often measured by repetition priming, in which performance on a task is facilitated for previously experienced items relative to new items. A commonly used test of implicit memory is a speeded classification task, in which subjects first encode a series of items by making a judgment about them (e.g., about their size or shape). Later, subjects are asked to make the same or a new decision as quickly as possible, and priming is seen if subjects are faster to make correct judgments for studied items relative to novel, baseline items. A growing body of findings indicates that at the initial encoding phase during these tasks, an incidental association is formed between the stimulus and the task-specific response required for that stimulus. This episodic association manifests as a reduction in priming when a new response is required during implicit testing, even if the test reengages the same abstract representation of the item (Dennis & Schmidt, 2003; Marsolek & Field, 1999; Poldrack & Cohen, 1997). This phenomenon is known as response specificity (Schacter, Dobbins, & Schnyer, 2004) or rapid response learning (Schnyer, Dobbins, Nicholls, Schacter & Verfaillie, 2006). The idea of rapid response learning is heavily modeled on Logan's (1988; 1990) instance theory, a prominent account of priming and automaticity of processing. According to instance theory, priming occurs as a function of a recorded *instance*, or a specific stored representation, of a previously encountered stimulus. Task-specific responses



on repeated items can become automatic if they are driven by a memory phenomenon in which the conclusion reached during the item's initial presentation is recovered, rather than by a recalculation of the original algorithm. Automaticity thus occurs in task environments that are consistent, such that practice with a specific solution to a specific problem forms a consistent mapping between the stimulus and its response. An important feature of this stimulus-response learning mechanism is that it is both incidental and associative. For this reason, studying rapid response learning offers a complementary way in which to test the status of incidental associative processing in aging.

To date, there is little evidence as to the status of rapid response learning in older adults. In young adults, evidence for rapid response learning in repetition priming has emerged from several recent studies (Dobbins, Schnyer, Verfaillie, & Schacter, 2004; Horner & Henson, 2008; Horner & Henson, 2009; Schnyer, Dobbins, Nicholls, Davis, Verfaillie & Schacter, 2007; Schnyer et al., 2006). In each of these studies, subjects performed an object classification task in which they were asked to decide whether the presented objects were bigger than a shoebox. Two speeded tests were later presented, one in which subjects made the same decision as previously, and one in which the cue was reversed, such that subjects were instructed to decide whether the objects were *smaller* than a shoebox. Importantly, reversing the classification from a bigger-than judgment to a smaller-than judgment should not impact the abstract knowledge representation of the stimulus. Rather, it is only the task-specific decision that must change in order to provide a correct response. A pattern of rapid response learning is demonstrated if cue reversal reduces priming. Each of these studies has provided evidence that at least some repetition priming on the speeded classification task could be explained by a stimulus-response (S-R) learning mechanism. Horner and Henson

(2009) recently found that when multiple levels of response learning were considered and controlled for (including not only the internal smaller-than/bigger-than conclusion but also the left/right finger mapping and the task-specific yes/no decision), S-R learning in fact accounted for all priming on the speeded classification task.

These recent findings present a challenge to some theoretical frameworks of implicit memory. For instance, research on the neural basis of implicit memory has shown that repetition priming is associated with decreased neural activation (also called response suppression) for previously studied stimuli relative to new stimuli. Depending on the technique, the reduction in hemodynamic response can be measured directly as decreased regional cerebral blood flow (using PET) or indirectly as decreased BOLD signal change (using fMRI). For instance, Henson, Shallice and Dolan (2000) presented a series of familiar faces and familiar symbols while subjects were instructed to search for a target. Simply viewing repeated faces or symbols was associated with decreased neural activity in fusiform gyrus. Such decreases in neural activity are typically interpreted to map onto the behavioral priming effect, as the facilitated, more efficient processing of previously studied stimuli.

According to a predominant model by Wiggs and Martin (1998), this decreased activation reflects a neural tuning, or sharpening, mechanism, in which only the neurons that respond best to the stimulus are recruited for re-processing that stimulus at a later time. The theory of neural tuning has been successful in explaining many instances of repetition priming, in particular visual specificity effects in which perceptual priming is sensitive to changes in the physical features of the stimulus (see Schacter, Wig & Stevens, 2007, for a discussion). However, the recent evidence of rapid response learning on speeded classification tasks does not fit as well within the framework of neural tuning. If priming

reflects a neural sharpening mechanism, then the re-presentation of the stimulus should be sufficient to produce neural priming, regardless of the decision cue. In contrast to this prediction, Dobbins, et al., (2004) found in an fMRI study that cue reversal reduced neural priming in both fusiform cortex as well as in left prefrontal cortex (PFC), but not in visual processing areas of extrastriate cortex. The neural priming effects in fusiform gyrus and left PFC were restored when a final classification task recapitulated the original cue. These findings indicate that although visual re-processing of the stimulus was undisturbed by cue reversal, the incidentally-learned stimulus-response association disrupted left PFC activity during the classification task. A similar result was found by Wagner, Koutstaal, Maril, Schacter and Buckner (2000), who showed that when the task remained consistent from study to test, decreased neural activations were found in left inferior PFC. However, the neural response suppression was eliminated when the task changed from study to test. These neuroimaging findings provide evidence against a neural sharpening mechanism, and instead suggest a system in which relying on a prior task-specific response reduces the overall executive processes required for the decision task in favor of a more automated response mechanism (Horner & Henson, 2009; Dobbins et al., 2004; Schacter et al., 2004).

Complementary evidence for this S-R learning mechanism comes from several studies (Dobbins et al., 2004; Horner & Henson, 2009; Schnyer et al., 2007) that have compared items presented multiple times at encoding (high-primed items) relative to items that were presented only once (low-primed items). Theoretically, stimulus-response learning should be strengthened for high-primed items, given their additional presentations and thus opportunities for S-R learning. In turn, cue reversal should have a larger impact (i.e., a larger reduction in priming) for high-primed relative to low-primed items. Consistent with these

predictions, Dobbins et al. (2004) found a larger priming reduction for high-primed relative to low-primed items, although significant slowing accompanied cue reversal for both high- and low-primed trials. Likewise, Horner and Henson (2009) found a significant priming reduction for high-primed items in three experiments, and a trend toward a larger priming reduction in high-primed items in their remaining experiments. These differences between the cue conditions indicate that multiple repetitions do not simply improve access to item-specific information but rather strengthen the relationship between the item and its associated response, through which a more automatic and efficient response strategy may be adopted.

Given the importance of S-R learning for extant theories of implicit memory, it is critical to determine the conditions under which evidence of S-R learning is and is not present, and whether it is apparent in different populations. Schnyer et al. (2006) tested the effect of cue reversal on patients with damage to the medial temporal lobes (MTL), which are critical for associative, or relational, processing (Cohen, Poldrack, & Eichenbaum, 1997; Konkel, Warren, Duff, Tranel, & Cohen, 2008). While the MTL-amnesic patients showed long-lag repetition priming to the same extent as healthy age-matched controls and young adults, their priming was not reduced by cue reversal, even following multiple repetitions. The insensitivity to reversing the decision cue indicates that the patients encoded the items but did not form an association between the items and their response, a mechanism that likely depends on the MTL.

This finding has important implications for older adults, for whom there is strong evidence of a disproportionate impairment in associative processing relative to the processing of item information (Chalfonte & Johnson, 1996, Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995). However, there may be important differences

between the relational deficit apparent in older adults and the one apparent in MTL-amnesic patients. One difference is that amnesiacs have often shown impaired relational memory under both intentional and incidental memory conditions (Chun & Phelps, 1999; Gooding, Mayes & Eijk, 2000; Ryan, Althoff, Whitlow & Cohen, 2000; Schnyer et al., 2006; but cf. Goshen-Gottstein, Moscovitch, & Melo, 2000), and there is recent evidence that all forms of relational processing are impaired by MTL-damage (Konkel et al., 2008). In contrast to amnesic populations, older adults have shown clear deficits under intentional encoding and retrieval conditions; however, not all forms of associative processing are equally affected. As described in previous sections, the status of incidental associative learning and memory is still uncertain. According to a meta-analysis by Old and Naveh-Benjamin (2008), studies comparing incidental and intentional learning conditions show a small overall age effect in explicit memory that follows incidental associative encoding, albeit a substantially larger effect under intentional conditions. However, there is some evidence that older adults show no difference in memory performance following incidental versus intentional encoding, but rather that young adults benefit more than older adults following intentional instructions (Hogan, Kelley & Craik, 2006). Such findings suggest that older adults can encode associations incidentally as well as young adults, and that the appearance of an age effect stems from a disproportionate improvement in the young following intentional instructions.

To understand the nature and source of the associative deficit in older adults, and to determine the ways in which this population differs from patients with medial temporal lobe damage, it is critical to delineate the conditions – both intentional and incidental – under which the deficit may appear. The recent evidence that S-R learning in speeded classification tasks reflects a type of incidental and automatized associative processing

provides an impetus to determine how cue reversal affects older adults. Experiments 4 and 5 of this dissertation examine whether older adults demonstrate rapid response learning.

## CHAPTER VIII.

### THE ROLES OF MTL AND PFC REGIONS IN ASSOCIATIVE MEMORY

A large body of research has identified medial temporal lobe structures as having a critical role in the formation of episodic memories (for reviews, see Cohen, Poldrack & Eichenbaum, 1997). The famous case-study of H.M., a patient who developed profound anterograde amnesia following surgical resection of major portions of his medial temporal lobe (MTL), led to the development of a framework that distinguished between declarative memory and nondeclarative memory. Declarative memory refers to a memory system dependent on the medial temporal lobe and which supports the formation of new episodic and semantic memories (i.e. memories that can be “declared”). Nondeclarative memory refers to a system independent of the medial temporal lobe and which supports varied learning functions such as motor, procedural and skill learning (i.e., functions that demonstrate learning but are not “declared” as memories) (see Corkin, 2002; Eichenbaum, 2002; Squire, 1992).

Since H. M., considerable evidence has emerged for a dissociation between declarative and nondeclarative memories in patients with MTL damage. In an initial demonstration, Warrington and Weizkrantz (1970) instructed amnesic patients to recognize words from an earlier study list; consistent with H.M., their performance was significantly lower than that of normal controls. In a separate test, the patients were asked to complete the (implicit) word stem completion task, and demonstrated priming equal to the normal controls. Similar results have been reported many times since Warrington and Weizkrantz’s

(1970) demonstration. (For reviews, see Shimamura, 1986; Carlesimo, 1999.) Investigations such as these helped lead to the characterization of declarative versus nondeclarative memories as explicit (retrieved consciously) and implicit (not retrieved consciously) (see Roediger, 1990; Schacter, 1987; Schacter & Tulving, 1994; Tulving & Schacter, 1990).

More recent research has supported the hypothesis that MTL amnesia produces a deficit in the ability to form *relations among elements* in a learning event, and that these relationships form the basis of the complex, contextually-specific, flexible representations that comprise declarative memories (Cohen, Poldrack, & Eichenbaum, 1997). This characterization supports a modification of the explicit/implicit distinction; a critical component of this hypothesis is that the medial temporal lobes will be involved in relational memory, regardless of whether these associations are tested directly (i.e., using conscious tests of explicit memory) or indirectly (i.e., using nonconscious tests of implicit memory) (Ryan, Althoff, Whitlow & Cohen, 2000). Recently, the hippocampus in particular has been shown to make a unique contribution to episodic memory by linking together various aspects of a learning event into a bound memory representation (Davachi, Mitchell, & Wagner, 2003; Eichenbaum et al., 2007; Giovanello, Schnyer & Verfaellie, 2004; but cf. Stark & Squire, 2003). Neuropsychological models based on lesion data suggest that the hippocampus serves to bind elements together into memory traces and operates both incidentally and obligatorily (Moscovitch, 1992).

Recent studies of amnesic patients with damage to the medial temporal lobes support this hypothesis that MTL amnesia is characterized by a deficit in the ability to form relations among elements, regardless of whether these associations are tested directly or indirectly (Cohen et al., 1997). For instance, Ryan et al. (2000) operationalized relational information



by manipulating the spatial location of a critical item within a picture. At test, amnesic patients and normal controls were asked to locate the critical item, and implicit relational memory was measured as an increase in eye movement or fixation toward the initial region of the item, relative to eye movement when asked to locate a novel item. A repetition priming effect was found both for normal controls and for the amnesic patients, with fewer fixations for repeated than for novel scenes. Only the normal controls showed the relational manipulation effect, however, in which the critical region in manipulated scenes received more fixations than the same regions in repeated or novel scenes. Amnesiacs showed no difference in these fixations. These results indicated that although the amnesic patients demonstrated intact repetition priming, relational memory was impaired even using a nonconscious measure. This pattern has emerged in several other studies of MTL-amnesic patients (e.g., Carlesimo, Perri, Costa, Serra & Caltagirone, 2005; Chun & Phelps, 1999; Park, Quinlan, Thornton, & Reder, 2004; For a contrary result, see Goshen-Gottstein, Moscovitch, & Melo, 2000).

A similar result was found by Chun (2005), who manipulated temporary (neuropharmacological, midazolam-induced) amnesia in healthy subjects. This study employed the contextual cuing paradigm, a visual search task in which subjects are instructed to search for a visual target among distractors, and relational priming is demonstrated if subjects are faster to detect a target within a previously seen contextual configuration relative to a new configuration. Subjects performed at chance levels when asked to distinguish explicitly between previously seen visual configurations and randomly generated new configurations, and performance was unaffected even by explicit instructions. Subjects demonstrated intact non-associative implicit memory in that their general search abilities

(procedural learning) improved across the task for both old and new configurations.

However, no relational priming was found. These results support the hypothesis that MTL structures are critical for relational processing under non-conscious conditions. A recent investigation using eye-tracking converges with neuropsychological and neuropharmacological studies positing the importance of the hippocampus for unaware relational memory (Hannula & Ranganath, 2009).

The recent evidence that some nonconscious learning functions are linked to the medial temporal lobes leads to a potential distinction between a form of implicit memory that depends on the MTL and a form of implicit memory that is independent of the MTL. A large body of research on the neural basis of implicit memory has shown that priming of single items is associated with decreased neural activation for repeated stimuli relative to new stimuli. Several theories have been put forth to account for these repetition-related decreases in activity. Experiments using nonhuman animals have shown that single neurons exhibit a reduced firing rate for repeated stimuli (Brown & Xiang, 1998), a finding that gave rise to the term “repetition suppression,” although this term is not always used in reference to the neural priming effect in humans. An analogue of repetition suppression in humans was put forward by Wiggs and Martin (1998) (based on Desimone, 1996) who posited a neural tuning, or sharpening, mechanism, in which only the most relevant neurons are selected to respond to a stimulus upon its reoccurrence, leading to faster mean firing rates. Other prominent accounts include fatigued neurons which exhibit lower amplitudes, or a reduction in the duration of neural activity (Grill-Spector, Henson & Martin, 2006; Henson & Rugg, 2003).

While neural deactivations reflect the typical neural signature of item priming mechanisms, the region of this response varies widely according to the type of stimuli and

type of task. Neural priming is typically evident in areas of stimulus- or concept-specific processing, such as extrastriate cortex of the occipital lobe (for visually perceived stimuli, e.g., Badgaiyan, 2000), fusiform cortex (for object or face stimuli, e.g., Henson, Shallice & Dolan, 2000), or left inferior prefrontal cortex (for priming of lexical or semantic information, e.g., Buckner et al., 2000; Wagner et al., 1997) (for reviews see Henson, 2003; Schacter, Wig & Stevens, 2007). Studies of patients with cortical lesions have provided double dissociations with patients with MTL-damage, and offer converging evidence that item priming depends on stimulus-specific cortical areas. For instance, patient M.S., who had lesions to occipital cortex, showed no priming on the (implicit) perceptual identification task in which subjects attempt to identify briefly presented words, despite unimpaired explicit memory (e.g., Gabrieli, 1995; for a review, see Schacter & Buckner, 1998b).

Although MTL structures have a well-supported role in relational processing, the prefrontal cortex (PFC) also serves an important role. Like the effect of MTL lesions (Ryan et al., 2000), lesions to (especially dorsolateral) PFC also produce larger deficits to relational memory than item memory (Stuss, Eskes & Foster, 1994). Moscovitch's (1992) component process model suggests that the frontal lobes are critical for the manipulation or organization of associations, including elaborative learning strategies that operate under effortful, intentional learning conditions. More recent research from functional neuroimaging provides convergent evidence that the MTL and PFC make important, though distinct, contributions to relational memory. While MTL structures have been associated with the incidental encoding and retrieval of contextual associations, the PFC has been associated with controlled processing of relational information, both at encoding (e.g., Henson, Shallice, Josephs & Dolan, 2002) as well as at retrieval (e.g., Badgaiyan, Schacter & Alpert, 2002; Velanova et

al., 2003; For a review, see Cabeza, 2006). Examples of controlled relational processes at encoding include the organization of inputs to the medial temporal lobe (Brewer, Zhao, Desmond, Glover & Gabrieli, 1998), whereas retrieval involves the monitoring or evaluation of contextual attributes (Hensen, Shallice & Dolan, 1999).

In one example (Rugg, Fletcher, Chua and Dolan, 1999), subjects completed an incidental deep encoding task in which they made animate/inanimate and pleasant/unpleasant judgments on word stimuli. Subjects later completed both an item recognition test as well as a source recognition memory test. fMRI analyses indicated that the source memory task engaged the left prefrontal cortex to a greater extent than the item recognition test. Similar results were found by Nolde et al. (1998a, 1998b), who showed that left PFC involvement was moderated to the extent that a task involved higher contextually-specific episodic retrieval demands.

Using event-related fMRI, Giovanello, Schnyer, and Verfaellie (2004) showed that the PFC is associated with a general attempt to retrieve relational details, while the hippocampus is critical for successful retrieval of associations. At study, participants simultaneously viewed two nouns and were instructed to create a sentence (covertly) that related the two words. At test, participants performed either an associative or an item recognition task. In the associative task, participants saw intact, recombined, and new word pairs, and were asked to indicate whether the two words were previously seen together. Analysis of the neuroimaging data revealed that, relative to item recognition, associative recognition resulted in activation of bilateral anterior hippocampus, as well as in a number of other regions including left inferior prefrontal cortex, bilateral temporal, and parietal regions. Follow-up region of interest (ROI) analysis of the mean activation level in bilateral anterior

hippocampus revealed greater activity when making associative judgments about intact pairs than in any other condition, suggesting that the hippocampus is critical for successful retrieval of relational information. In contrast, ROI analysis of the mean activation level in left PFC revealed significant activity both for the intact and recombined pair conditions, consistent with the notion that left inferior PFC activation is related to more general strategic processes associated with relational retrieval attempt. Similarly, Dobbins, Foley, Schacter and Wagner (2002) showed that, relative to item memory, attempt to retrieve the encoding condition under which the item was acquired (i.e., source memory) was dependent on left PFC, even though this activity was independent of source memory accuracy.

## CHAPTER IX.

### NEURAL BASIS OF IMPLICIT ASSOCIATIVE MEMORY

Although the role of the PFC in implicit memory for new associations has not been systematically investigated, it is likely that tests implicit associative memory may correspond with PFC regions if they concurrently involve strategic or evaluative processes. For instance, Badgaiyan, Schacter and Alpert (2003) conducted a PET study in which participants studied unrelated word pairs and were subsequently tested on associative word stem completion (WSC). Increased regional cerebral blood flow (rCBF) in right MTL was observed in the same context relative to the same different condition, consistent with other studies on the neural basis of relational priming. However, both the same and different context conditions (relative to fixation) were associated with increased rCBF to left frontal gyrus. This finding coincides with research from the associative recognition literature (e.g., Giovanello et al., 2004), which has shown that frontal activation is associated with a general attempt to retrieve relational information. The frontal activation during associative WSC provides important convergent evidence for the behavioral literature, in which this task has been sensitive to encoding manipulations that affect explicit processes. Such findings suggest caution in the use and interpretation of priming in this task, especially for studies of age differences.

In contrast, tests of implicit associative memory that do not appear to involve strategic or explicit processes have been consistent with neuropsychological studies that highlight the importance of the MTL in the processing of relational information. In a study of nonconscious semantic associative retrieval, Henke et al. (2003) had subjects view face-

profession pairs that were flashed subliminally (below the threshold of conscious awareness) between visual masks. At test, subjects were asked to indicate whether the general semantic category of each face's profession had been an artist or academic. Accuracy for the categories test was at chance, yet subjects were faster to make correct guesses relative to incorrect guesses. On control trials, for which a profession was assigned to each face but was not presented to the subjects, there was no reaction time difference between correct and incorrect guesses. The RT difference for correct and incorrect face-profession pairs was taken as a measure of unaware semantic associative retrieval. Neural activity associated with this contrast revealed increases in bilateral hippocampus as well as right perirhinal cortex. The involvement of these MTL regions coupled with the direction of activity (increases, rather than deactivations) was thus fundamentally different from the neural basis of item priming. Henke and colleagues extended these findings in a more recent paper (Degonda et al., 2005), which showed increased activity in anterior hippocampus and right perirhinal cortex during subliminal (non-conscious) associative encoding.

However, recent findings from Yang, Mecklinger, Xu, Zhao and Weng (2008) conflict with findings from Henke and colleagues (2003; Degonda et al., 2005). At encoding, subjects viewed two Chinese characters (familiar word stimuli for the subjects) and judged their orthographic similarity. The maximum amount of time allotted to each subject for each encoding trial was set such that it would yield only 20-40% correct on a subsequent recognition test, thus precluding the possibility of explicit contamination. The implicit test measured reaction time to reading intact (i.e., presented together), recombined (presented at study but not together) and new character pairs. Associative priming was defined as the overlap in neural activations for intact-recombined and intact-new contrasts. Associative

recognition was measured as neural activity for correct old responses (hits) minus correct recombined responses (correct rejections). Bilateral hippocampus and parahippocampal cortex were active during the explicit associative measure. However, the hippocampus was not involved in associative priming, and the direction of activity for adjacent MTL structures was the opposite from what Henke et al. (2003) had found: implicit associative memory was correlated with *decreased* activity in right parahippocampal cortex (PHC), as well as anterior cingulate cortex, inferior frontal gyrus, and occipital cortex.

It is uncertain what accounts for the divergent findings between Henke et al. (2003) and Yang et al. (2008). Yang et al. (2008) questioned whether that the active involvement of the hippocampus found by Henke et al. (2003) may have resulted from explicit processing. Indeed, while the prototypical neural signature of priming is a reduction in activity, the RT difference for correct relative to incorrect guesses found by Henke et al. was associated with increased neural activity, more typical of explicit retrieval. However, the chance-level accuracy on the retrieval task used by Henke et al. (2003) coupled with the fact that stimuli were presented below the level of awareness at encoding make the possibility of explicit contamination unlikely, if not impossible. Moreover, the hypothesis that active hippocampus indexes explicit processes per se has been challenged by a wide body of research in the neuropsychological as well as fMRI domains, which have shown the hippocampus to be involved in relational processing independently from awareness or intention (Ryan et al., 2000; Chun & Phelps, 1999; Hannula & Ranganath, 2009).

An interesting alternative possibility is that the difference between Henke et al. (2003) and Yang et al. (2008) is a reflection of different kinds of relational information. Specifically, it is possible that the hippocampus and adjacent MTL structures are



differentially engaged during implicit retrieval of conceptual (Henke et al.) versus perceptual (Yang et al.) associations. There is evidence from the explicit memory literature that a differential network of neural regions is activated during semantic versus perceptual associative retrieval. Prince, Daselaar and Cabeza (2005) found that while successful explicit retrieval of semantic (word-word) and perceptual (word-font) associations both involved the hippocampus, semantic retrieval also involved left ventrolateral PFC while perceptual retrieval involved right posterior parahippocampal gyrus, left occipitotemporal cortex and bilateral parietal cortex. To date there is no direct evidence as to whether implicit retrieval of conceptual and perceptual associations may engage different neural regions, or even elicit a different direction of neural response. Experiment 6 in the present series of studies tested the possibility that differences between Henke et al. (2003) and Yang et al. (2008) could be due to differences in conceptual versus perceptual associative processing.

## CHAPTER X.

### EFFECTS OF AGING ON THE NEURAL BASIS OF IMPLICIT RELATIONAL MEMORY

As described earlier, successful associative encoding and retrieval supporting *explicit* relational memory appear to be a function of both hippocampal-mediated binding mechanisms as well as strategic, consciously controlled prefrontal mechanisms (e.g., Degraanges et al., 1998; Gabrieli et al., 1997; Giovanello et al., 2004). It is also likely that successful relational memory depends not only on unique contributions of PFC and MTL regions, but also on the functional connectivity between them (Cabeza, 2006). Several lines of research have indicated that both PFC and MTL regions are affected by aging, both in terms of region-specific activity, as well as a decreased correlation between the regions (Grady et al., 1995; Mitchell et al., 2000; Park & Gutchess, 2005; Stebbins et al., 2002).

Regarding PFC, aging is associated with pronounced and reliable changes in frontal cortical regions. The frontal aging hypothesis was developed based on strong neuropsychological data of non-pathological aging that has linked multiple age-related cognitive declines with prefrontal dysfunction (Moscovitch & Winocur, 1995). Evidence for PFC dysfunction in aging has also been evident in studies of functional neuroimaging using PET and fMRI. For instance, Anderson et al. (2000) found that a divided attention manipulation in young adults during word pair encoding mimicked aging, such that weaker activity was found in left PFC in young adults under divided attention but in older adults under full attention. PFC reductions have been found in older adults for temporal relational

memory as well. In a PET investigation (Cabeza et al., 2000) subjects completed both an item recognition test and a recognition test of temporal order. Older adults performed disproportionately worse on the temporal order task than the item task. Consistent with this pattern, temporal order retrieval was associated with greater left PFC activity relative to item retrieval in young but not older adults. Taken together, such findings fit with the hypothesis that episodic memory declines are, at least in part, associated with fewer processing resources and mediated by weakened prefrontal activity.

Regarding MTL regions, aging is sometimes associated with smaller MTL volumes in structural studies, as well as overall decreased MTL activation in functional studies, across different types of tasks (for a review, see Raz, 2000). However, there is mixed evidence as to whether or not weakened MTL activity is directly linked with age-related episodic memory declines. Using fMRI, Giovanello et al. (2009) recently showed that young adults elicited greater hippocampal activity than older adults during accurate retrieval of relational compound word conjunctions. During picture encoding, Gutchess et al. (2005) found weaker parahippocampal cortex activity coupled with increased activity in inferior frontal regions in older compared with younger adults. Likewise, using PET, Grady et al. (2005) found age-related reductions during word retrieval in hippocampal activity, coupled with increased activity in PFC. These studies provide evidence that that age-related memory declines are linked with MTL dysfunction. In contrast, however, other studies have shown age-related preservations in MTL. For instance, using PET, Cabeza et al. (2000) observed equivalent MTL activation between older and younger during word retrieval. Likewise, using fMRI, Miller et al. (2008) and Rand-Giovanetti et al. (2006) both found preserved hippocampal activation during associative face-name encoding. In summary, the literature currently offers

an inconsistent pattern in which MTL activity is only sometimes reduced in older compared to younger adults during episodic memory tasks. It is uncertain what accounts for these discrepancies. One possibility is that different subregions within the MTL may be differentially affected by aging. For instance, there is some evidence that aging is associated with larger decrements in the hippocampus relative to the rhinal cortex, both in terms of functional activity (Daselaar et al., 2006) as well as structural volume (Yonelinas et al., 2007). A related possibility is that distinct processes of episodic memory that are differentially affected by aging may differentially engage the MTL (for a review, see Daselaar & Cabeza, 2008). For instance, Daselaar et al. (2003) found weaker hippocampal activity in older adults during deep but not shallow encoding. Moreover, because the hippocampus has been shown to be more involved in relational memory and recollection, whereas the rhinal cortex has been shown to be more involved in item memory and familiarity (Brown & Aggleton, 2001; Davachi et al., 2003; Ranganath et al., 2004; Yonelinas, 2002), the dissociated effect of age on different structures within the MTL is consistent with theoretical frameworks of age-related episodic memory decline (Jacoby, 1999; Naveh-Benjamin, 2000) that have emerged from behavioral studies. Further data are needed to clarify the discrepancies and delineate which episodic memory processes will or will not be associated with weakened MTL function.

To help inform this question, Experiment 6 in the present series of studies tests whether the effects of age on MTL function are similar during implicit and explicit retrieval of new associations. Regarding explicit associative retrieval, MTL and PFC regions will likely both contribute to age-related declines, to the extent that this form of memory requires both item-context binding as well as strategic manipulation or organization of these features.

The critical question is whether MTL dysfunction will be evident on an implicit task that should be independent from strategic processes mediated by the PFC. Some research suggests that on tasks that engage the hippocampus but do not involve concurrent strategic processes that require the engagement of the PFC, no age differences in neural activity will emerge (Head et al., 2005; Hedden & Gabrieli, 2005). To date, only one published study has investigated implicit relational memory in aging from a cognitive neuroscience perspective, and its findings are consistent with this possibility. Using ERP, Trott, Friedman, Ritter, Fabiani, and Snodgrass (1999) showed no age differences behaviorally on a speeded recognition task for same-context and different-context noun pairings, coupled with large age decrements on a subsequent explicit source judgment. Consistent with the behavioral results, the ERP indexes showed no age differences on the early-onset speeded old-new judgment, but age-related differences emerged in the late onset, long duration, frontally-oriented activity that was associated with the source judgment. The timing of this activity was interpreted within Moscovitch's (1992; 1994) component process model, in which the earlier, old-new effect could be associated with an MTL-mediated, automatic, non-strategic judgment, and the later, old-new effect could be associated with a PFC-mediated, strategic, effortful search or retrieval of source information. Based on these findings, it would appear reasonable to predict that no age differences in regions of neural activity, including the MTL, should emerge during a test of unintentional, nonstrategic relational retrieval.

Complicating this prediction, however, is one of the most interesting puzzles in the cognitive neuroscience of aging literature: the reorganization of the structure-function relationship that appears to accompany healthy aging, with reduced activations in task-related regions coupled with increased activations in non-task-related regions. One example of this

reorganization concerns changes in hemispheric lateralization, such that on tasks that engage the left hemisphere in young adults, older adults tend to engage bilateral regions. For instance, whereas young adults show activity in left PFC during semantic encoding, older adults show left PFC activity as well as contralateral activity in right PFC (Morcom, Good, Frackowiak & Rugg, 2003; Stebbins et al., 2002). This empirical pattern has been generalized as the Hemispheric Asymmetry Reduction in Older Adults model (HAROLD, Cabeza, 2002, see also Reuter-Lorenz & Stanczak, 2000) and has been found across varying paradigms (Backman et al., 1997; Cabeza et al., 1997; Logan et al., 2002; Madden et al., 1999; Rosen et al., 2002). A second example of the structure-function reorganization in healthy aging is the posterior-anterior shift (PASA, reviewed by Davis et al., 2008), such that older adults show a reduction in activity in posterior regions (e.g., occipital cortex) coupled with increased activity in anterior regions (e.g., PFC). Like HAROLD, PASA has been demonstrated in several types of paradigms, including visual perception (Grady, et al., 1994; Madden & Hoffman, 1997), attention (Cabeza et al., 2004; Madden et al., 2002), working memory (Rypma & D'Esposito, 2000), and episodic memory (Grady et al., 2002; Madden et al., 1999). A relevant extension of PASA is that it occurs for neural deactivations. Davis et al. (2008) found that older adults elicited less deactivation in posterior midline regions (part of the default network in which midline regions are deactivated during cognitive tasks compared with baseline rest conditions, Raichle et al., 2001) coupled with additional deactivations in anterior midline regions.

The function (i.e., purpose) of these age-related changes in neural architecture has been challenging to interpret. One hypothesis is that neural changes that accompany cognitive tasks are a function of *dedifferentiation*, such that there is an age-related

breakdown in the specialization of neural regions supporting cognitive tasks and/or an inability to inhibit prefrontal response (Grady et al. 1995; Logan et al., 2002; Persson et al., 2007). For instance, Morcom, Li and Rugg (2007) found a similar pattern of neural activity between young and older adults when source memory performance was matched through additional stimulus presentations. However, older adults showed fewer concurrent retrieval-related deactivations, consistent with the hypothesis of a decline in the efficiency of processing. An alternative hypothesis is that neural changes are a function of successful aging, such that recruitment in non-task related frontal regions *compensates* for declines in more posterior regions (Cabeza et al., 2002). Evidence supporting the compensation account has emerged from several studies showing that activation in task- and non-task related regions correlate positively with behavioral performance in older adults (Dennis et al., 2008; Rajah & D'Esposito, 2005; Rajah & McIntosh, 2008; Reuter-Lorenz & Lustig, 2005). A third hypothesis is that older and younger adults use different component processes to support performance on a cognitive task (Morcom, et al., 2007). For instance, Daselaar et al. (2006b) found that although overall recognition accuracy was equated between age groups, recollection contributed more to young adults' retrieval, whereas older adults relied more on familiarity. Unambiguous support for any of these viewpoints is a current challenge in the literature, and it is possible that more than one of these hypotheses can operate concurrently, depending on the task employed.

An important question is whether neural changes are unique to cognitive tasks that are impaired in aging, or whether neural differences will appear even on tasks in which no difference is found behaviorally. One way in which this question has been examined has been to equate behavioral performance by providing older adults with strategies or additional

stimulus presentations to improve their performance (e.g., Daselaar et al., 2006c; Marcom et al., 2007). A caveat of such methods is that it systematically varies the encoding operations undertaken by the two age groups, and subsequent retrieval differences become more difficult to interpret. An alternative method is to compare neural activity differences on tasks that are preserved in aging. Such studies overcome the common difficulty in identify whether neural activation differences are due to aging or to task performance. Given the substantial age differences found in a wide variety of cognitive tasks, very few studies employ this method. However, there is some evidence of neural activations differences even on tasks of preserved cognitive function. One example is from Grady et al. (1999), who found that older adults showed weaker MTL activity than young adults during incidental picture encoding, even though picture memory was not impaired in older adults on the behavioral accuracy measure. More recently, Bergerbest et al. (2009) compared older and younger participants on a conceptual implicit speeded abstract/concrete judgment task in which no age difference was found behaviorally. Older adults showed less repetition-related deactivation in left inferior PFC, but showed additional deactivations not shown by young adults in right inferior and middle PFC, middle frontal cortex, and anterior cingulate. These additional activation reductions in right frontal regions correlated with priming scores as well as with independent vocabulary scores, supporting the viewpoint that right (i.e., contralateral to young adults) PFC engagement is associated with successful aging.

Experiment 6 of the present series of studies investigated whether older and younger adults would show a similar or different pattern of neural activity during implicit relational retrieval, using a task in which behavioral equivalence is expected. This study documents the first fMRI analysis of implicit relational memory in older adults, coupled with a within-



subjects comparison with explicit relational memory that followed the same encoding manipulation

## CHAPTER IX.

### EXPERIMENT 1

The primary goal of Experiment 1 was to determine whether older adults could show priming for new conceptual associations, using a novel speeded response paradigm that was designed to minimize strategic encoding or retrieval processes that could artifactually produce age differences. My approach was to use a paradigm based on McKoon and Ratcliff (1979). In their study, subjects first encoded a series of unrelated word pairs. Later they complete a speeded lexical decision task for words that appeared either alongside their studied associate, or next to a different studied word. Associative priming was demonstrated by faster performance for words within the intact pair relative to the recombined pair. In the present experiment, subjects performed an associative version of an object classification task. In the standard version, size judgments are made for presented objects relative to a standard-sized referent object, such as a shoebox, and are later asked to make the same decision again as quickly as possible (e.g., as used in Buckner et al., 1998; Dobbins, Schnyer, Verfaillie, & Schacter, 2004; Horner & Henson, 2009; Koutstaal, Wagner, Rotte, Maril, 2001; Schnyer, Dobbins, Nicholls, Davis, Verfaillie & Schacter, 2007). The present experiment employed an associative version of this task. In the current paradigm, subjects judged whether two presented objects were, together, smaller than the referent object (a desk drawer). The implicit test was a speeded version of the same task, using intact (presented together), recombined (each presented but not together), and new object pairs, thus mirroring the conditions in a prototypical associative recognition test. This task, described in more detail

below, was selected for two reasons: 1) Incidental tasks are less likely than intentional tasks to invoke differential use of encoding strategies (Park & Gutchess, 2005); 2) Speeded response tasks are more likely than accuracy tasks to reflect automatic processes, based on the assumption that automatic processes are engaged faster than consciously controlled processes (Horton, Wilson & Evans, 2001; Horton, Wilson, Vonk, Kiry & Nielson, 2005; Yonelinas & Jacoby, 1994), and appear to be less prone to explicit contamination (Light et al., 2000; Prull, 2004). If the associative memory decline in older adults stems from a deficit in relational processing that affects both encoding and retrieval, then young but not older adults will show associative priming. If, however, the associative memory decline stems from a deficit in strategic retrieval of relational information, then no age differences in associative priming will emerge.

## Method

### *Participants*

Thirty-six young adults (ages 18-21,  $M = 18.5$ ,  $SD = .77$ ; mean education = 13.3 years,  $SD = .91$ ) participated in partial fulfillment of a course requirement in an Introduction to Psychology course at the University of North Carolina at Chapel Hill. Twenty-four older adults (ages 65-87,  $M = 76.5$ ,  $SD = 5.6$ ; mean education = 16.3 years,  $SD = 1.95$ ) were recruited from the local community and were paid \$10 per hour. Prior to participation, the older adults received a general health screen completed a battery of neuropsychological tests to assess memory, language, attention, visuo-spatial abilities, and general intellectual functioning. These tests included the Mini Mental State Examination (MMSE), American National Adult Reading Test (ANART), Trail Making Test parts A and B, Vocabulary from the WAIS-III, and the Morningness-Eveningness questionnaire. Mean scores for participants

in Experiment 1 as well as all subsequent Experiments are listed in Table 1.

### *Design and Materials*

The stimuli consisted of basic drawings of familiar objects taken from the Microsoft Online Clip-Art Database and the website <http://www.clipart.com>. The line drawings were colored in one of eight singular, plausible real-world colors (e.g., a blue couch; a red shoe) to maximize similarity across items on complexity and visual-perceptual characteristics. The colors were manipulated systematically using Adobe Photoshop. All materials were pilot-tested for clarity of object depiction and for consistency in classification response. Trials consisted of two objects, presented side-by-side.<sup>1</sup> Objects were randomly paired together with the constraint that they did not have a pre-existing semantic relationship. In total (across subjects), each object appeared in either the left or right screen location an equal number of times. Objects that appeared on the left at encoding also appeared on the left at retrieval, regardless of whether it was presented in an intact or recombined pair. Each object was framed by a simple line box. Pairs were counterbalanced across retrieval conditions using the Latin square method, although a few replacements were made so that each list would produce approximately 50% yes responses and 50% no responses to the classification task. The counterbalance produced 12 study lists and 12 corresponding test lists composed of intact, recombined, and critical new object pairs. The study list began with 8 practice pairs followed by 24 critical pairs, and ended with two additional buffer pairs to reduce recency effects. The

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<sup>1</sup> The study and test lists in Experiment 1 also included trials in which only single, colored objects appeared. None of these objects overlapped with objects in the associative trials. Questions related to the single objects are being followed in a separate project. For this reason, the results and theoretical analysis of the single object priming are not included in the present paper. However, for an accurate methodological description it is critical to note that a single object condition was included in Experiment 1. On these trials, subjects were instructed to make a standard size judgment rather than the associative version. At test, subjects completed a speeded version of the same task. Subsequent experiments did not include this condition.

test list included the 24 study pairs, half of which were presented as intact pairs, and half of which were rearranged with each other to create recombined pairs, plus 24 unstudied critical new pairs. To decrease the likelihood that subjects would notice the overlap in the actual stimuli that were presented, 20 additional filler pairs were added to the test. Filler pairs are different from new pairs in that they are not counterbalanced and thus not included in analysis, but they serve to increase the ratio of new to old trials and decrease the connection from the subject's perspective between the study and test portions of the experiment. Order of the test pairs was randomized with the constraint that it began with two filler pairs. The experiment was presented on an Apple iBookG4 using the program MacStim (WhiteAnt Occasional Publishing). All data were collected via computer key-press.

### *Procedure*

Participants were tested individually in a quiet, enclosed room. After obtaining informed consent to participate, the experiment was described as being concerned with object perception and knowledge. No mention was made of an ensuing memory test. Participants were instructed to view the presented objects and decide, by pressing Y or N on the computer with their dominant hand, whether the objects would fit together in a desk drawer of 1' X 2' dimensions. A desk drawer of this size was provided for each participant's direct reference. Instructions emphasized that the judgment should be based on the typical real-life size of the presented objects. Each trial remained on the screen for 8000ms at which point the next trial was presented. After the incidental deep encoding task, participants then completed a distractor task, in order to minimize recency effects or rehearsal as well as the connection between the study and test portions of the experiment. The distractor task consisted of solving anagram word puzzles and lasted five minutes. After the puzzles were collected,

subjects completed the implicit retrieval test, in which they were asked to complete the object classification task again, as quickly as possible, without sacrificing the accuracy of the response. This task was described as being interested in how we make quick decisions about information in our environment. After a response was pressed for each trial, the objects were cleared from the screen and were replaced with a fixation cross, which remained on the screen until the next trial was presented, always 4000ms from the onset of the prior trial. The subjects were instructed to keep their eyes focused on the cross, because the next trial would appear there, and this would make it easier to respond quickly.

Following the implicit test, an awareness questionnaire was administered (see Barnhardt & Geraci, 2008, for a recent positive assessment of the validity of these questionnaires). Awareness questionnaires probe whether subjects were aware of the connection between the study and tests portions of the experiment, and are typically included in studies of implicit memory in order to test for the possibility of explicit contamination. Critically, prior findings in the literature suggest that it is not awareness itself that affects associative priming, but rather the adoption of an explicit retrieval strategy that may occur once subjects become aware of the study-test connection. McKone and Slee (1997) compared performance on an associative lexical decision task between subjects who were test-aware but who continued to follow the implicit test instructions, with subjects who were test-aware but who, upon awareness, altered their approach to the task and attempted to recall studied items directly. The authors found a difference in priming between these two groups, with the former group producing the same pattern as those who were unaware, and the latter group producing the same pattern as those who were explicitly instructed to recall the studied words. Given these findings, those who reported awareness of the connection between the

study and test pairings in the present experiment were subsequently asked whether they consciously attempted to think back to their prior responses during the speeded task. Performance was later compared between those who did and did not claim to have used an explicit retrieval strategy, so as to test for the possible influence of explicit contamination.

### *Results and Discussion*

Priming scores were submitted to a mixed ANOVA, with pair type (intact, recombined, new) as a within-subjects factor and age as a between subjects factor. A significant effect was followed by planned comparisons between recombined and new conditions to determine item priming, and between intact and recombined conditions to determine associative priming. These within-subjects comparisons were conducted separately for each age group. Priming effects (i.e., RT differences and standard errors) for Experiment 1 and all subsequent experiments are listed in Table 10.

Mean accuracy for the classification task during the implicit test was high for both age groups (young adults = 95.4%; older adults = 91.8%). Mean reaction times and standard deviations for each condition on the implicit test are listed in Table 2, with outliers of +/- two standard deviations from the mean in each condition removed from analysis for each subject. There was a significant main effect of trial type ( $F(2,116) = 25.28, p < .001$ ), indicating that response times varied as a function of condition. There was no interaction between age and trial type ( $F(1,116) = 1.07, p = .347$ ), indicating that the difference among the retrieval conditions was not moderated by age. Planned contrasts revealed that significant item priming was found for recombined relative to new pairs for both younger ( $t(35) = -2.45, p < .05$ ) and older ( $t(23) = -2.17, p < .05$ ) adults. Importantly, significant associative priming was found for intact relative to recombined pairs in both younger ( $t(35) = -3.36, p < .01$ ) and

older ( $t(23) = -2.39, p < .05$ ) adults. There was a main effect of age on the RT data (i.e., older adults demonstrated higher baseline RTs, consistent with general cognitive slowing, see Salthouse, 1996). As such, priming was also calculated as percent change from baseline, with young adults producing  $m = 7.1\%$  ( $sd = 1.4$ ) decrease in reaction time for recombined relative to baseline pairs and older adults producing  $m = 4.7\%$  ( $sd = 1.3$ ) decrease, with no priming difference between the age groups using the measure of percent change,  $p = .51$ . For associative priming, young adults produced  $m = 6.3\%$  ( $sd = 1.1$ ) decrease in RT from recombined to intact pairs and older adults producing  $m = 7.4\%$  ( $sd = 1.6$ ), with no difference between the age groups,  $p = .75$ .

Twenty-nine young adults reported having noticed a connection between the study and test pairings. Of these, 11 of these subjects reported having used an explicit retrieval strategy to aid performance on the test. Twenty-three older adults reported noticing the study-test connection, 7 of whom reported use of an explicit retrieval strategy. These numbers raise the concern that priming performance may have been mediated by explicit processing. To examine this possibility, test-awareness and reported strategy use were entered into separate mixed ANOVAs as between-subjects factors, with RTs to the retrieval conditions (intact, recombined, or new) entered as a within-subjects factor. There was no interaction between retrieval condition and awareness of the connection between study and test portions of the experiment,  $F < 1$ , and no interaction between retrieval condition and the reported use of explicit retrieval,  $F < 1$ . However, given the small number of subjects when split into the above subgroups, it is possible that these comparisons suffer from a lack of power to determine reliable differences. For this reason, the pattern of reaction times was compared between those who did and did not claim to have used an explicit retrieval strategy, and are



displayed in Table 3. The direction of performance was the same for both groups, with RTs to intact pairs faster than to recombined, which were faster than baseline. These analyses show that the pattern of priming performance did not depend on whether the participant claimed to use an explicit retrieval strategy. These results stand in contrast to the pattern that has emerged for other conceptual associative priming tasks (e.g., in McKone & Slee, 1997), and provide evidence that intentionally thinking back to prior responses is not useful for performance in the present paradigm.

Lastly, when only the reaction times to accurate responses were included in the analyses, the pattern of all reported results remained unaffected. This is not surprising, given the near-ceiling levels of accuracy. However, it was critical to make sure that neither age group demonstrated a trade-off between speed and accuracy.

These results indicate that older adults can show priming for new conceptual inter-item associations using picture stimuli and a speeded, incidental task. Because both age groups were sensitive to the context change (i.e., the difference between intact and recombined pairs), the priming data provide evidence that the older adults did initially encode the associations. Although some have argued that a lack of age deficits in priming can be a function of a lack of power, the raw RT difference score for both item priming as well as associative priming was actually in the direction of being greater for the old than young adults. As such, insufficient power is an unlikely explanation for the lack of age differences. These data provide evidence against a general deficit in relational processing that emphasizes impairments at both encoding and retrieval. Rather, they imply a role of conscious or strategic retrieval processes in the typically observed age deficit. These results fit with a more general pattern in the literature of spared implicit or automatic processes in aging

(Light et al., 2000), even for conceptual-associative materials on which explicit impairments are often found.

Although the results of Experiment 1 are interpretable within this theoretical framework, several components of the design merited follow-up. First, although the task was designed to assess object knowledge (i.e., typical size of the real-life object, rather the size of what was visually perceived on the screen), the finding of associative priming on this task leaves open two possible interpretations: 1) Associative priming may have been driven by a facilitation in making the conceptual size judgment; alternatively 2) Associative priming may have been driven by a facilitation in visually perceiving the objects together. Therefore, it is unclear whether associative priming on this task validly reflected the reengagement of conceptual, rather than perceptual, operations. Experiment 2 was designed in part to address these issues by examining whether the pattern of age equivalence would emerge on a semantic task that more validly assesses category knowledge. Experiment 2 also included a manipulation check to determine whether the pattern of reaction time performance would be sensitive to changes in the perceptual form of the presented objects.

A second limitation of Experiment 1 was that, although the object classification task was designed to be integrative by instructing participants to decide whether the objects would fit into the drawer *together*, it is plausible that the subjects reached their decisions by engaging in a sequence of item-specific processes. That is, it is plausible that subjects came to each classification decision by deciding, first, whether the left object would fit, and subsequently, whether the right object would fit. This would be especially problematic on some trials, as certain individual items (e.g., a couch) could negate the need to perceive its paired associate, and a nominally pair-wise response could be made simply on the basis of

the first item. In turn, it is possible that some of the overall priming was driven by item-specific, rather than relational, processing. Experiment 2 improved on this potential limitation by using a categorization task that related the objects more consistently to each other. The task was changed from one in which both items of a pair are judged relative to a separate referent object, to one in which a relative judgment is made only between the critical stimuli. This change made the task more relational, and precludes responses based only on the representation of single items. Pilot-testing for the new task in Experiment 2 also allowed us to reduce the stimulus onset asynchrony to 6000ms.

Lastly, a goal of the present set of studies was to test whether implicit memory for conceptual associations could be dissociated from strategic, explicit conceptual- associative processes. Although the age equivalence found in the preliminary experiment implies a role of conscious, strategic retrieval processes in the typically observed age deficit, it does not provide direct evidence of this hypothesis. Importantly, some studies have shown that age differences, even in explicit associative memory, can be minimized under incidental relative to intentional encoding conditions. Hogan, Kelley and Craik (2006) found that the interaction between age and type of encoding was not driven by improved performance within older adults under incidental conditions; on the contrary, older adults showed no difference in memory following the two conditions. Instead, the interaction was explained by younger adults benefiting more than the older adults following intentional encoding, with this boost in the younger adults creating the appearance of an age effect. Such findings suggest that older adults can encode associations incidentally as well as young adults, even when tested explicitly. However, other findings have shown reliable age differences under incidental conditions, albeit smaller than under intentional conditions (see meta-analysis by Old &

Naveh-Benjamin, 2008). Therefore, the effect of age on incidental encoding remains unclear. For this reason, it was critical in Experiment 2 to include a within-subjects comparison with explicit, associative recognition, in order to determine whether the typical age decline in recognition accuracy is found using the same materials and following the same incidental encoding task.

## CHAPTER XII.

### EXPERIMENT 2

Experiment 2 tested three primary questions. The first question was whether the age equivalence found in Experiment 1 would generalize to a new associative semantic classification task, described in more detail below. The second question was whether the measure of associative priming validly reflected a facilitation in making the semantic judgment, or whether it reflected a facilitation in processing surface-level, perceptual information. Experiment 2 was designed to clarify this issue in two ways. First, the object decision task changed to one that has been demonstrated in prior studies to be insensitive to changes in perceptual form. Specifically, the new associative semantic categorization was *which of two objects is more likely to be found inside a house*. An item-level version of this task was examined by Bruce, Carson and Burton (2000), who presented a different exemplar of objects at study and test. This global change in perceptual form had no impact on the amount of priming (measured as the speeded inside-outside judgment). The second way in which Experiment 2 was designed to clarify differences between perceptual and conceptual influences in the priming measure was to determine directly whether the associative version of this task is also insensitive to perceptual alterations. To serve as this manipulation check, some of the objects at test appeared in a different color than their initially studied form. Because older adults have been shown to perform similarly to young adults on tests of perceptual-associative priming (Light et al., 1992; Monti et al., 1997), it is critical to

determine whether associative priming in this task reflects, at least in part, the reengagement of perceptual analysis.

The third primary question addressed in Experiment 2 was whether a within-subjects dissociation would be found between conceptual associative priming and explicit, associative recognition. If so, this dissociation would provide more direct support for the hypothesis of spared conceptual implicit associative retrieval processes coupled with impaired explicit retrieval associative processes in aging. Moreover, an age difference in recognition but not priming following the identical incidental encoding manipulation would contradict the possibility that the typical age-related impairment in associative recognition is simply a function of deficient intentional encoding.

## Method

### *Participants*

Thirty-two younger adults (ages 18-33,  $M = 20.9$ ,  $SD = 3.3$ ; mean education = 14.8 years,  $SD = 1.7$ ) and 32 older adults (ages 61-89,  $M = 73.5$ ,  $SD = 5.9$ ; mean education = 16.8 years,  $SD = 2.6$ ) participated in Experiment 2. None of the subjects in Experiment 2 had participated in Experiment 1. The young adults participated in partial fulfillment of a course requirement in an Introduction to Psychology course at the University of North Carolina at Chapel Hill. Older adults were recruited from the local community and received \$10 per hour to compensate participation. Health screening and eligibility criteria remained the same as in Experiment 1.

### *Design and Materials*

Pilot-testing created ratings on a scale of 1-5 for each object as a function of likelihood of being found inside a house. These ratings were used to construct object

pairings, such that at least a two-point rating difference existed between paired objects. This system created pairs for which a consistent, but not necessarily obvious, inside-outside judgment would be made on every trial. Trials consisted of two objects, presented side-by-side. Each object was framed by a simple line box. In each task, the object more likely to be found inside a house appeared on the left side of the screen in 50% of the trials and on the right side of the screen in the remaining 50% of trials. Each object's relative location remained constant from study to test. For the perceptual manipulation check, a second version of all pairs was created in which each object appeared in a modified color. The colors in both versions of the object pairings represented plausible real-world colors for each object; thus, this perceptual manipulation did not affect the abstract conceptual representation of the object or its task-specific classification.

The first encoding list included 5 practice pairs followed by 30 critical pairs, and ended with 2 recency buffer pairs. The implicit test list included 10 counterbalanced critical new pairs plus the 30 studied pairs, 10 of which were intact, 10 of which were recombined, and 10 of which were color-manipulated versions of pairs that were otherwise intact (studied together). The recombined trials were constructed such that an object's relative classification status did not change from study to test; thus although the objects were presented in a new context, the response mapping for each object remained constant. Twenty-three additional filler pairs were added to the list, which, like in Experiment 1, served to increase test length and the ratio of new to old trials in order to decrease the connection from the subject's perspective between the study and test stimuli. List order was randomized with the constraint that it began and ended with two filler pairs. The second encoding list, to be matched with the explicit test, began and ended with two buffer pairs, and included 20 critical pairs that

were not presented in the first two tasks. The explicit recognition test included these 20 encoded pairs, 10 of which were intact and 10 of which were recombined, plus 10 counterbalanced critical new unstudied pairs. Individual stimuli were unique to each condition for individual subjects. Pairs were counterbalanced using the Latin Square method such that, across subjects, pairs appeared in each condition an equal number of times. This counterbalance produced 7 list versions for each task.

### *Procedure*

During the first encoding task, subjects decided which of two presented objects was more likely to be found inside a house. Subjects recorded their choice by pressing either the j or k keys (labeled as “left” and “right”) with their dominant hand. Each trial remained on the screen for 6000ms. This encoding task was followed by a three-minute distractor task in which subjects were asked to work on anagram puzzles. Subjects then completed the implicit test, in which they were instructed to complete the object decision task again, as quickly as possible, without sacrificing the accuracy of the response. After key-pressing a response for each trial, the objects were cleared from the screen and replaced with a fixation cross, which remained on the screen until the next trial was presented, always 4000ms from the onset of the prior trial. Subjects were instructed to keep their eyes focused on the cross, because the next trial would appear there, and this would make it easier to respond quickly. The implicit test was followed by the awareness questionnaire. A second incidental encoding task was next, which was set up identically to the first, with the exception that a new set of object pairs was presented. After another 3-minute distractor task consisting of arithmetic problems, subjects completed the explicit, associative recognition test. Subjects viewed each object pair and were asked to decide whether the pair was *seen together previously*. Subjects recorded



their choice by pressing either the “i” or “o” key, which were labeled as “Yes” and “No” respectively. After a response was made, the objects were cleared from the screen and were replaced with a cross, which remained until the next trial was presented, with an SOA of 6000ms. Participants were told that if they did not make their choice within 6 seconds, the next trial would appear; however, it was emphasized that they should feel free to use all the time available to make their best decision.

### *Results and Discussion*

Like Experiment 1, mean accuracy on the classification task was high for both age groups (young adults = 97.6%; older adults = 95.3%). Data analysis for item and associative priming involved the same procedures as in Experiment 1. Mean reaction times and standard deviations for each implicit trial type are listed in Table 2. Using a mixed ANOVA with trial type (intact, recombined, recolored, and new) as a within-subject factor and age as a between-subjects factor, there was a significant main effect of trial type for both young ( $F(3, 186) = 48.20, p < .001$ ), indicating that response times varied as a function of condition. There was also a significant interaction between trial type and age group, ( $F(3, 186) = 4.14, p < .01$ ). Planned follow-up pairwise contrasts were conducted to determine individual priming effects as well as the source of the interaction. Significant item priming (i.e., for recombined relative to new pairs) was found in both younger ( $t(31) = -5.26, p < .001$ ) and older ( $t(31) = -4.54, p < .01$ ) adults. When the age groups were compared with each other, older adults in fact produced more item priming to an extent that was marginally significant ( $t(62) = 1.78, p = .080$ ). Importantly, significant associative priming was found for intact relative to recombined pairs in both younger ( $t(31) = -2.99, p < .01$ ) and older ( $t(31) = -2.41, p < .05$ ) adults. When compared with each other, there was no difference in the amount of

associative priming between young and older adults,  $p = .23$ . Lastly, no difference was found between intact and re-colored pairs in young ( $p = .34$ ) or older ( $p = .70$ ) adults, showing that reaction times were not affected by the perceptual manipulation. Consistent with findings from Bruce, et al. (2000) who used the single item version of the inside/outside classification task, the comparison between intact and re-colored trials here indicated no sensitivity in priming for either age group to the visual form of the objects.

Thus, the source of the interaction between trial type and age group in the omnibus test appeared to be a function of greater item priming in the older adults. One possibility for this finding is that age differences might be magnified by the use of raw RT difference as the measure of priming, given the slower overall RTs in older adults. To examine this possibility, priming was also calculated as percent change from baseline, with young adults producing  $m = 11.7\%$  ( $sd = 1.3$ ) decrease in reaction time for recombined relative to baseline pairs and older adults producing  $m = 13.0\%$  ( $sd = 1.6$ ) decrease. The difference between these was not significant,  $p = .72$ . Thus, there was no age difference in item priming when using the measure of percent change. For associative priming, young adults produced  $m = 3.9\%$  ( $sd = 1.0$ ) decrease in RT from recombined to intact pairs and older adults producing  $m = 4.9\%$  ( $sd = 1.5$ ), with no difference between the age groups,  $p = .74$ . Like Experiment 1, insufficient power to detect reliable age differences is not a viable explanation for the results, as the raw RT scores were in the direction of greater differences in old than young. This pattern is somewhat unexpected given that general slowing accounts (e.g., Salthouse, 1996) might suggest that speeded access to semantic information may be impaired in aging, despite preservations in general semantic knowledge (e.g., Burke & MacKay, 1997). However, the present data show that this general possibility does not impact priming, at least using this

paradigm.

We also examined whether priming was affected by the possible influence of explicit retrieval, as assessed by the awareness questionnaire. Twenty-nine young adults reported having noticed a connection between the study and implicit test pairings, with 9 of these subjects reporting use of an explicit retrieval strategy. Twenty-nine older adults also reported noticing the study-test connection, 11 of whom reported use of an explicit retrieval strategy. Using the awareness questions as between-subjects factors in separate mixed ANOVAs, test-awareness and explicit strategy use did not participate in any significant effects ( $F < 1$ ) for either question in either age group. Reaction times for each trial type as a function of explicit strategy use were compared and are included in Table 3. The same overall pattern was produced by those who did and did not claim to use an intentional retrieval strategy, with reaction times to intact pairs faster than to recombined, which were faster than baseline. Like Experiment 1, the pattern of priming in both age groups suggests that there is limited utility of an explicit retrieval strategy for this paradigm. Lastly, a correlational analysis was run between associative priming and associative recognition scores, to determine whether subjects who demonstrated better recognition memory would also produce more priming. There was no relationship between performance on the two tests in young adults ( $r = .12, p = .51$ ) or old adults ( $r = .04, p = .85$ ).

For the explicit test, mean proportions of hits to intact pairs, false alarms to recombined pairs, and false alarms to new pairs are listed in Table 4. A measure of item recognition accuracy was calculated as the proportion of hits to intact pairs relative to the proportion of false alarms to new pairs. Associative recognition accuracy was calculated as the proportion of hits to intact pairs relative to false alarms to recombined pairs. As stated

earlier, this analysis method has been successful in isolating associative memory from item memory, because all the units within intact pairs and recombined pairs have been studied – the only difference between them is how the information was paired. If participants encode both elements individually, but have difficulty integrating them together into a cohesive unit, then hit rates to intact pairs will be high, but recombined pairs will likely elicit false alarms, and will in turn decrease accuracy. Using a mixed ANOVA with accuracy (item versus associative) as a within-subjects factor and age as a between subjects factor, there was a significant main effect of accuracy ( $F(1, 62) = 1154.74, p < .001$ ). Follow-up pairwise contrasts revealed that item accuracy was significantly higher than associative accuracy, ( $t(63) = 30.12, p < .001$ ), although item and associative accuracy were each significantly greater than zero in young ( $t(31) = 32.27, p < .001$  and  $t(31) = 6.46, p < .001$ , respectively) and older ( $t(31) = 34.45, p < .001$  and  $t(31) = 2.35, p < .05$ , respectively) adults. Additionally, there was a significant interaction between accuracy and age in the omnibus test ( $F(1, 62) = 18.2, p < .001$ ), indicating that the difference between item and associative accuracy was moderated by age group. Follow-up contrasts revealed a larger difference between item and associative accuracy in older adults relative to younger adults,  $t(61) = 4.24, p < .001$ . Furthermore, young and older adults showed no difference in hit rates to intact pairs ( $p = .19$ ) or in false alarms to new pairs ( $p = .17$ ), but young adults produced significantly fewer false alarms to recombined pairs than the older adults, ( $t(62) = -5.73, p < .001$ ) This pattern produced an interaction ( $F(1, 62) = 18.19, p < .001$ ), such that the age groups showed no difference in item recognition accuracy ( $p = .93$ ) coupled with the typical benefit for young adults in associative recognition accuracy,  $t(62) = 4.24, p < .001$ . Although this interaction was significant, interpretations are limited by the fact that item memory was at ceiling for both age groups.

Thus, the present experiment cannot provide definitive support for a disproportionate deficit in associative recognition relative to item recognition. However, a larger impairment in associative memory than item memory has been reliably replicated in many previous studies (see Spencer & Raz, 1995 and Old & Naveh-Benjamin, 2008 for meta-analyses), and the critical comparison for present purposes was between associative recognition and associative priming.

I also explored the possibility that the hit and false alarm rates on the explicit measure could have been influenced by reported use of an explicit retrieval strategy on the implicit measure. By design, the explicit test always followed the implicit test. If subjects became aware of the connection between the encoding and test stimuli, and if they consequently thought back to prior responses during the implicit test, this could influence the way they approached the subsequent encoding task despite the incidental instructions. The hits to intact pairs, false alarms to recombined pairs and false alarms to new pairs are broken down by reported explicit strategy use status in Table 3. Interestingly, while strategy use had a negligible effect on the subsequent explicit test in older adults, it appears that young adults who used explicit retrieval on the implicit test had both higher hits as well as higher false alarms on the explicit test. This increase in both hits and false alarms indicates that while strategy use on the implicit test did not affect accuracy on the explicit measure, it did change response bias in young adults such that they became more likely to endorse both old and new pairs as “old.” This change in response bias has little impact on the main interpretation of the age effect in the present experiment; however, variables that differentially affect response bias in young and old adults are an important avenue for future research.

In summary, Experiment 2 generalized the results of Experiment 1 to a different

semantic classification task. This pattern provides convergent evidence that older adults can show priming for conceptual item-item associations using a paradigm that removes potentially confounding strategic processes from both encoding and retrieval. Importantly, although some studies have shown no or minimal age differences in explicit memory following incidental encoding (Hogan, et al., 2006; Naveh-Benjamin et al., 2009) the present incidental encoding manipulation was only associated with age equivalence on the implicit retrieval measure. In contrast, an age effect did emerge following the same encoding task on the explicit, associative recognition test, coupled with no difference on the item recognition test. The age-related dissociation between explicit and implicit memory also argues against explicit contamination on the implicit task; if an explicit retrieval strategy were to aid performance on the implicit test, it would have benefitted the younger adults. Within the associative recognition data, the age difference in accuracy was driven by a disproportionately high rate of false alarms to recombined pairs. This pattern fits with the viewpoint that the individual items are familiar at retrieval, but that the older adults cannot use recollection of contextually-specific attributes as well as young adults to reject recombined lures (e.g., Jacoby, 1999). Taken together, the results in Experiment 2 demonstrate that the lack of age differences in associative priming cannot be explained only as a function of equivalent incidental encoding. Rather, the results are consistent with a pattern of unimpaired automatic retrieval processes, such as implicit memory and item familiarity, and emphasize a deficit in the explicit, strategic recollection of associative information.

## CHAPTER XIII

### EXPERIMENT 3

As described earlier, the speeded response paradigm in Experiments 1 and 2 was designed to be more likely to tap into unintentional, non-conscious response mechanisms than the associative priming paradigms used previously in the literature. The equivalent priming between the age groups suggests that performance on the implicit task was, indeed, not contaminated by explicit retrieval processes. However, many findings in the young adult literature have found difficulty in dissociating explicit associative memory from conceptual-associative implicit memory using standard tasks such as associative word stem completion (McKone & Slee, 1997; Schacter & Buckner, 1998). Specifically, when the formation of associations occurs via the semantic integration of distinct items, associative priming has shown to be sensitive to encoding manipulations that affect explicit retrieval processes, such as levels-of-processing manipulations (Graf & Schacter, 1985; O'Hanlon, Wilcox & Kemper, 2001; Reingold & Goshen-Gottstein, 1996), or divided attention (Kinoshita, 1999), and has sometimes found only for test-aware subjects (Bowers & Schacter, 1990). Given this pattern in the young adult associative priming literature, it was critical to provide more direct evidence convergent with the age effect that performance on the present measure of associative implicit memory could not be explained by the involvement of explicit processes. For this reason, Experiment 3 was implemented in order to test whether the measure of implicit conceptual-associative memory used in Experiments 1 and 2 could be empirically

dissociated from strategic, explicit conceptual-associative memory in young adults. If so, this would provide strong evidence against the possibility of explicit contamination.

To determine whether a functional dissociation between implicit and explicit memory might emerge using the priming paradigm, the effects of incidental vs. intentional encoding were compared between associative priming and explicit, associative recognition. Based on findings in the item priming literature (e.g., Neill et al., 1990), I predicted that intentional encoding would improve recognition performance relative to incidental encoding, but this manipulation would have little or no impact on priming.

## Method

### *Participants*

Forty-eight younger adults (ages 18-21,  $M = 18.7$ ,  $SD = .76$ ; mean education = 13.0 years,  $SD = .83$ ) participated in Experiment 3. None of the subjects had participated in either Experiment 1 or 2. Subjects received credit for a course requirement in an Introduction to Psychology course at the University of North Carolina at Chapel Hill.

### *Design and Procedure*

The stimuli and list set-up were identical to those used in Experiment 2. The variable of incidental versus intentional encoding was manipulated within subjects and the variable of implicit versus explicit memory was manipulated between subjects. Each subject received two study-test blocks, consisting of either incidental-implicit followed by intentional-implicit, or incidental-explicit followed by intentional-explicit. The experiment began with the incidental encoding task, in which subjects were asked to decide *which of the two presented objects was more likely to be found inside a house*. Trials remained on the screen for 6000 ms, regardless of the timing of response. Following a 3-minute distractor task, half



the subjects completed a surprise associative recognition test and half the subjects completed the associative priming task. For associative recognition, participants viewed a series of object pairs and were asked to decide whether the pair was *seen together previously*. On the priming test, participants were asked to complete the object categorization task again, as quickly as possible, without sacrificing the accuracy of the response. The retrieval task was followed by a second encoding task, in which subjects were asked to make the inside/outside judgment a second time. They were additionally instructed that there would later be a memory test, and that as they made their decision they should try to remember the way in which the objects were paired. After another 3-minute distractor task, subjects completed either a second associative recognition task or a second associative priming task. Following the second associative priming task, subjects completed an awareness questionnaire in which they indicated whether they noticed a connection between study and test stimuli, and whether they intentionally tried to think back to previous responses, on either (or both) versions of the reaction time tests. To avoid potential contamination, an awareness questionnaire was not administered after the first implicit test.

### *Results and Discussion*

The results of the implicit test blocks are presented here first. Mean reaction times in each retrieval condition for subjects assigned to complete the implicit memory tests are listed in Table 6. As in Experiments 1 and 2, outliers of +/- two standard deviations from the mean in each condition for each subject were removed from analysis. There was a significant overall effect of implicit trial type following both the incidental ( $F(2,46) = 25.49, p < .001$ ) and intentional ( $F(2,46) = 10.11, p < .001$ ) encoding conditions, showing that reaction time varied as a function of trial type. Importantly, there was a significant interaction between

implicit trial type and encoding condition, ( $F(2,46) = 14.25, p < .001$ ), showing that the overall pattern of priming differed between incidental and intentional encoding. Planned contrasts between each pair of trial types revealed the following pattern of findings: No difference was found for baseline reaction time to new pairs on the implicit test between incidental encoding ( $RT = 1163$  ms) and intentional encoding ( $RT = 1168$  ms),  $p = .90$ . Following the incidental condition, significant item priming was found (i.e., for recombined relative to new pairs),  $t(23) = -4.22, p < .001$ , as well as significant associative priming (i.e., for intact relative to recombined pairs),  $t(23) = -2.67, p = .01$ . Following the intentional encoding condition, significant item priming was again observed ( $t(23) = -5.41, p < .001$ ). Importantly, however, no associative priming was found,  $p = .86$ .

The remaining 24 subjects who did not complete the implicit test blocks were assigned to the explicit test block condition. Mean proportions of hits to intact pairs, false alarms to recombined pairs, and false alarms to new pairs are listed in Table 6. As in Exp. 2, item recognition accuracy was measured as proportion of hits to intact pairs minus proportion of false alarms to new pairs, and associative recognition accuracy was measured as proportion of hits to intact pairs minus proportion of false alarms to recombined pairs. The encoding manipulation had no impact on item recognition ( $p = .65$ ), with  $.84$  ( $SE = .06$ ) accuracy following incidental encoding, and  $.85$  ( $SE = .05$ ) accuracy following intentional encoding. This nonsignificant difference is not surprising, given the near-ceiling level of item recognition accuracy, and moreover, given that the intentional instructions emphasized focusing on the way in which the objects were paired. This coincides with previous studies showing that when subjects are instructed to focus attention on associative pairings rather than individual item units, associative recognition greatly benefits, with little or no impact on

item recognition (Hockley & Cristi, 1996, Naveh-Benjamin, 2000). Importantly, associative recognition accuracy was significantly improved when moving from incidental encoding (accuracy = .22,  $SE = .047$ ) to intentional encoding (accuracy = .41,  $SE = .052$ ),  $t(23) = -2.87$ ,  $p < .01$ .

On the awareness questionnaire (administered only after the second implicit test but inquiring about both tests), 21 subjects indicated having noticed the connection between the encoding tasks and the subsequent reaction time tasks. Of these, 15 subjects indicated that they attempted to use an explicit retrieval strategy to aid performance on the first implicit test, and an additional 2 subjects (i.e., 17 total) claimed to have used an explicit retrieval strategy on the second implicit test. The magnitude of associative priming did not depend on having claimed this explicit strategy for the incidental condition ( $p = .18$ ) or for the intentional condition ( $p = .76$ ).

It is uncertain, based only on the data in Experiment 3, what cognitive mechanism underlies the dissociative effect of incidental versus intentional encoding on implicit and explicit associative memory. One possible explanation for the disrupted priming is that intentional encoding more closely overlapped with the cognitive operations involved in explicit relative to implicit retrieval. Increases in the overlap in cognitive operations from study to test is often shown to improve memory performance, according to principles of transfer-appropriate processing (though see Masson & MacLeod, 2002, and Mulligan & Dew, 2009, for examples in which TAP does not account for memory performance). Additionally, cues (both internal and/or external) available at encoding can benefit memory performance if available again at test (encoding specificity principle, see Tulving & Thompson, 1973). In the present study, the intentional encoding instructions were open-

ended, such that subjects could have adopted myriad cognitive strategies at encoding. For instance, consider the situation in which subjects adopt an encoding strategy of creating a sentence or a visual image that meaningfully links the two objects. If subjects think back to that sentence or image at test, the reengagement of this cue should aid in recognition. However, thinking back to a sentence or image would likely not aid performance on an “unrelated” implicit object classification test, such that taking the time to recall an internally generated sentence or image would likely slow down, rather than enhance speed of response (see also Horton et al., 2001).

In summary, although future data are needed to delineate what drives the elimination of associative priming following intentional encoding, Experiment 3 provides strong evidence against the possibility of explicit contamination in the paradigm employed. While moving from incidental to intentional encoding elicited a large improvement in associative recognition performance, the same experimental manipulation eliminated associative priming. This dissociation demonstrates that functional independence between explicit and implicit associative memory can be found using the speeded classification paradigm. Although the present experiment demonstrated this effect in young adults, it would be of substantial theoretical interest in future research to determine whether incidental versus intentional encoding has a similar effect on older adults. More generally, however, the results suggest that prior evidence of functional similarities between associative priming and explicit memory (e.g. McKone & Slee, 1997; Schacter & Buckner, 1998) may have reflected processes specifically involved in the selected tasks, and do not reflect more general features of conceptual associative implicit memory.

## CHAPTER XIV

### EXPERIMENT 4

Experiments 4 and 5 examined the status of rapid response learning, a complementary form of incidental associative processing that has received much recent attention in the literature, especially in regards to speeded classification tasks (Dobbins et al., 2004; Horner & Henson, 2008, 2009; Schnyer et al., 2006, 2007). The first goal of Experiment 4 was to determine whether healthy older adults show evidence of rapid response learning to the same extent as younger adults. As described previously, studies of associative memory in aging (e.g., Naveh-Benjamin, 2000) have provided strong evidence that older adults have an impairment in the formation and retrieval of associative links, especially during intentional encoding and retrieval tasks. However, there have been mixed findings as to the status of incidentally formed associations, with incidental associative processing sometimes preserved in older adults (e.g., Hogan, Kelley & Craik, 2006) and sometimes impaired (Old & Naveh-Benjamin, 2008). Thus, testing rapid response learning is an important way to determine the extent of the associative deficit in older adults. Of note, Schnyer et al. (2006) found that while reversing the decision cue reduced priming in young adults (i.e., demonstrating response learning), cue reversal did not impact priming in MTL-amnesiacs. In that study, healthy age-matched controls ( $n=12$ , mean age = 55.1 years) showed evidence of response specificity with high-primed items but there was not a significant priming reduction for low-primed items. Although this could indicate that the controls required multiple presentations in order to bind together the items with their response, it is unclear whether a significant priming reduction following only one stimulus presentation might emerge using a task that

accesses a pre-existing category.

A second goal of Experiment 4 was to determine whether prior findings of rapid response learning in young adults (Dobbins et al., 2004; Horner & Henson, 2008; Schnyer et al., 2006; 2007) would generalize to a new speeded classification task. In the majority of previous studies, the task instructed participants to decide whether the presented object was bigger or smaller than a shoebox. Horner and Henson (2009) observed that size, in this context, does not reflect a pre-existing category but rather a relative judgment that is assessed only during the experimental setting. Thus, it is possible that such a classification task would maximize the likelihood that an episodic association would be formed between the object and the task-specific response. In contrast, a classification task that relies more on prior semantic knowledge may be less likely to produce as strong an episodic association, and could in turn reduce the effect of rapid response learning on priming. Horner and Henson (2009) observed that size, in this context, does not necessarily reflect a pre-existing category but rather a relative judgment that is assessed during the experimental setting. Thus, it is possible that such a classification task would maximize the likelihood that an episodic association would be formed between the object and the task-specific response. In contrast, a classification task that relies more on prior semantic knowledge may be less likely to produce as strong an episodic association, and could in turn reduce the effect of rapid response learning on priming. Horner and Henson (2009, experiment 2) showed that cue reversal reduced priming using a man-made versus natural decision task, providing a generalization of S-R learning to a classification task more dependent on prior semantic knowledge. The present experiment tested whether cue reversal reduces priming using the inside/outside classification task. Before testing the status of rapid response learning on the associative version of this speeded

classification task (Experiment 5), Experiment 4 first tested whether cue reversal would reduce priming using a single item version of the task.

## Method

### *Participants*

Twenty-four younger adults (ages 18-25 years,  $M = 20.0$ ,  $SD = 2.1$ ; mean yrs education = 13.9,  $SD = 1.6$ ) participated in partial fulfillment of a course requirement in an Introduction to Psychology course at the University of North Carolina at Chapel Hill. Twenty-four older adults (ages 64-85 years,  $M = 73.8$ ,  $SD = 7.3$ ; mean yrs education = 16.6,  $SD = 2.1$ ) were recruited from the local community and were paid \$10 per hour to compensate participation. Eligibility criteria remained the same as the prior experiments. None of the subjects had participated in Experiments 1-3.

### *Design and Materials*

The stimuli consisted of the same colored line drawings of familiar objects that were used in Experiments 1-3, with the exception that only single objects were presented, rather than pairs. In total, there were 140 objects which were counterbalanced using the Latin Square method across two study-test blocks, one in which the implicit test required the same classification response as at study and one in which the decision cue was reversed. This counterbalance produced 4 list versions for each task. Half the subjects were randomly assigned to complete the same-cue block first and the other half completed the reverse-cue block first. The stimuli were divided pseudo-randomly with the constraint that each list produced approximately 50% yes responses and 50% no responses to the classification task. Each of the two encoding lists began with 4 practice pairs (in which the experimenter could provide feedback to ensure adherence to the instructions), followed by 2 primacy buffers, 35

critical trials, and ended with 2 recency buffers. Each of the two retrieval lists included the 35 studied trials and 35 baseline critical new trials, plus 28 filler trials that served to decrease the connection between the study and test portions of the experiment. Order of the test pairs was randomized with the constraint that it began and ended with two filler trials. During the encoding tasks, trials remained on the screen for 6000ms regardless of the timing of response, after which the next trial was presented automatically. During the retrieval tasks, trials disappeared from the screen as soon as a response was pressed, and were replaced by a crosshair which remained on the screen until the onset of the next trial, with a total ISI of 4000ms. The experiment was presented on an Apple iBookG4 using the program MacStim (WhiteAnt Occasional Publishing).

### *Procedure*

Participants completed the experiment individually in a quiet, enclosed testing room. After obtaining informed consent, the experimenter explained that subjects were going to complete a series of activities concerned with how we perceive and classify everyday objects and how this relates to problem solving abilities. The experiment began with the first encoding task. Subjects were instructed to view each object and decide, by pressing the keys labeled as “yes” or “no” (the z and x keys) whether the object is typically found inside a house. Participants were told that they should respond “no” for objects that could *possibly* be found inside a house but are *typically* found elsewhere (e.g., a basketball). Following the encoding task, participants completed a four-minute distractor task consisting of anagram puzzles. For subjects assigned to complete the same-cue condition first, the next task was the speeded classification task in which they were instructed to make the same decision as earlier, as quickly as possible, without sacrificing the accuracy of the response. The second



encoding task was completed next and was identical to the first with the exception that a new set of objects was presented. Another four-minute distractor task was completed next and consisted of arithmetic puzzles. The second implicit retrieval task followed; if completing the reverse-cue condition, participants were instructed to view the presented objects and decide *whether each object is typically found outside a house*.

### *Results and Discussion*

Mean reaction times and standard deviation for each condition are displayed in Table 7. Outliers of more than two standard deviations from the mean were removed from each condition for every subject. Similar to other studies of response learning (e.g. Horner & Henson, 2009; Schnyer et al., 2007), only correct (i.e., consistent) responses were included in analyses. The removal of outlying and inconsistent responses resulted in the exclusion of 3.6% of the total trials in young adults and 5.2% of total trials in old adults. Collapsing both retrieval tasks, older adults had slower baseline reaction times than younger adults ( $t(46) = -3.65, p = .001$ ), consistent with general cognitive slowing (Salthouse, 1996). Using a mixed ANOVA with baseline reaction times (same-cue versus reverse-cue) as a within-subjects factor and age as a between-subjects factor, there was a significant overall effect of cue reversal on baseline reaction times,  $F(1, 46) = 14.74, p < .001$ , demonstrating a cost associated with task switching, consistent with trends in some previous studies (e.g., Schnyer et al., 2007). There was no interaction between age and switch costs,  $F < 1$ . Follow-up  $t$ -tests showed more specifically that young adults produced slower responses to baseline trials in the reverse-cue condition relative to the same-cue condition ( $t(23) = -3.59, p < .01$ ). Cue reversal similarly affected older adults, to an extent that approached significance ( $t(23) = -2.00, p = .057$ ).

Priming was measured as a decrease in reaction time to studied trials relative to baseline critical new trials, and rapid response learning was measured as a decrease in priming for cue reversal relative to when the cue remained the same from study to test. As with the prior experiments, mean priming effects are presented in Table 10. Using a 3-way ANOVA with factors of age, priming (i.e., old vs. new), and cue condition (i.e., same vs. reversed), there were significant effects of priming, ( $F(1, 46) = 67.84, p < .001$ ) and cue condition ( $F(1, 46) = 31.20, p < .001$ ). There was a significant interaction between priming and cue condition, ( $F(1, 46) = 11.40, p < .01$ ), with larger priming effects for the same-cue relative to reversed-cue condition. There was no interaction between priming and age ( $F < 1$ ), or between cue condition and age ( $F < 1$ ), and no three-way interaction between priming, cue condition, and age ( $F < 1$ ). In summary, both young and older adults demonstrated significant priming (relative to zero) in same- and reversed-cue conditions, as well as a significant priming reduction in the reverse-cue condition. These results demonstrate that both age groups formed an episodic association between the objects and their task-specific response.

Experiment 4 showed that young and older adults demonstrated equivalent priming on the speeded classification task in the same-cue condition, consistent with findings from Experiment 2. The finding of age-related preservations in same-cue priming is important for present purposes because reductions in priming following cue reversal can be attributed to S-R learning rather than to an age-related difficulty in the classification decision. Indeed, the results showed that priming in both young and older adults was equally affected by cue inversion, demonstrating rapid response learning in both age groups. The equivalent impact of cue reversal on both age groups indicates that the older adults were able to form the

stimulus-response association spontaneously and as quickly as the young adults. The pattern of rapid response learning was produced on a new semantic classification task that accesses a pre-existing knowledge category that is possibly less ad-hoc than the size judgment task used in prior studies (see also Horner & Henson, 2009, for a similar finding). The reduction in priming observed in the present study demonstrated that, on this task, only one stimulus presentation was necessary for participants to form an episodic association between the object and the response required for that object, for both young and old adults. These findings present a new example of a form of associative processing that is spared in aging, and fit with the recent suggestion that despite marked age-related impairments in many measures of associative memory (Naveh-Benjamin, 2000), not all forms of associative processing are equally affected by aging (Old & Naveh-Benjamin, 2008).

However, an alternative possibility for the age-equivalence found in Experiment 4 is that the formation of association between a single stimulus and its required response may have been too simple to detect reliable differences. There is evidence from the working memory literature that age-related impairments in feature binding are compounded by cognitive load (Mitchell, Raye, Johnson & D'Esposito, 2000a), with memory performance declining even when the number of features increased from one to two. Furthermore, Gagnon, Soulard, Brasgold, and Kreller (2007) found a direct correlation, with older adults' memory for contextual details (e.g., color or size) decreasing as the number of features increased, a finding that was attributed to decreased attentional resources. This interpretation fits with complementary studies (Braver, Satpute, Keys, Racine & Barch, 2005; Glisky, Rubin & Davidson, 2001) that highlight the importance of frontal lobe functioning in the encoding and maintenance of context information. The negative correlation between

relational complexity and performance (Gagnon et al., 2007; Mitchell et al., 2000a) suggests that in a more complex classification paradigm, older adults may have fewer processing resources than young adults to form a stimulus-response association with only one stimulus presentation.

## CHAPTER XV

### EXPERIMENT 5

Experiment 5 tested whether age differences in rapid response learning would emerge in a more complex speeded classification paradigm, specifically one that assesses priming of novel associations. Experiments 1 and 2 showed that on a speeded associative classification task using intact and recombined pairs, older adults produced as much priming as young adults. However, it is unclear whether forming an associative link between the object stimuli occurred at the expense of an additional link between the stimuli and their task-associated responses. Furthermore, there is evidence that older adults' relational memory performance declines with the number of features to be associated (Gagnon et al., 2007; Mitchell et al., 2000a). For this reason, while both age groups would likely show associative priming when the cue remains the same, it was possible that only young adults' associative priming would be impacted by cue inversion.

Experiment 5 also contributes to the young adult literature in its assessment of the effect of rapid response learning in associative priming. The vast majority of research in rapid response learning has been examined in terms of item (i.e., repetition) priming. To date, the only example of an associative decision task that was used to test stimulus-response learning is from Dennis and Schmidt (2003). In their study, subjects viewed pairs of unrelated words (e.g., elephant-jeep, desk-flowerpot, thimble-squirrel) and decided which was larger. Later, reaction times were compared for trials in a re-pair match condition (recombined items that required the same item-specific response, e.g., desk-squirrel) with a

re-pair mismatch condition (recombined items that required the opposite item-specific response, e.g., desk-jeep). Reaction times were faster for the re-pair match condition relative to the re-pair mismatch condition. This finding coincides with the recent studies of rapid response learning (Schnyer et al., 2007; Horner & Henson, 2008, 2009), in that performance was facilitated for trials in which subjects could rely on prior item-specific responses. Because Dennis and Schmidt (2003) used a size judgment, however, the paradigm is potentially limited by the same characteristic of other size classification tasks, in that the semantic decision is rather extemporaneous, thus perhaps maximizing the potential formation of an episodic association. The present study tested whether response learning would impact priming using the associative version of the inside/outside judgment.

Additionally, as described in the previous experiments, the set-up of an associative priming paradigm that uses intact and recombined pairs also offers a complementary measure of item priming. Specifically, because both constituent objects in the recombined pair have been seen previously, facilitated task performance for recombined relative to new pairs provides a measure of item memory in the absence of associative memory. Although this RT difference can be interpreted to represent item priming, this form of item priming differs critically from standard versions of repetition priming, in that the pair (i.e., the complete stimulus) is not actually repeated from study to test. Importantly, rapid response learning has as of yet only emerged when the stimulus is repeated in its exact form. For instance, Schnyer et al. (2007) found that cue reversal did not reduce priming when a different object exemplar was presented at test, even though the task-specific classification should not vary between different exemplars. Given this finding, Experiment 5 tested the possibility that an instantiation of item priming that does not involve whole stimulus-level repetition might not

be affected by cue reversal.

## Method

### *Participants*

Thirty-two young adults (ages 18-22 years,  $M = 19.7$ ,  $SD = 1.2$ ; mean yrs education = 12.8,  $SD = 1.2$ ) and 32 older adults (ages 65-83 years,  $M = 72.1$ ,  $SD = 6.1$ ; mean yrs education = 16.4,  $SD = 2.2$ ) participated in Experiment 5. None of the subjects in Experiment 5 had participated in prior Experiments. The young adults participated in partial fulfillment of a course requirement in an Introduction to Psychology course at the University of North Carolina at Chapel Hill. Older adults were recruited from the local community and received \$10 per hour to compensate participation. Health screening and eligibility criteria remained the same as previous experiments.

### *Design and Materials*

The stimuli were the same as Experiment 2, with objects presented side-by-side. Like Experiment 4, half the subjects were randomly assigned to complete the same-cue block first and the other half completed the reverse-cue block first. Each of the two encoding lists included 4 practice pairs followed by 20 critical pairs, and ended with 2 recency buffer pairs. Each corresponding implicit test list included 10 counterbalanced critical new pairs plus the 20 studied pairs, 10 of which were presented as *intact pairs* (i.e., presented together previously), and 10 of which were rearranged with each other to form *recombined pairs*. The recombined trials were constructed such that an object's relative classification status did not change from study to test. Thus, although the objects were presented in a new context, the response mapping for any given object remained constant. Twenty additional filler pairs

appeared on each implicit test, which, like in Experiment 1, were not included in analyses but served to increase test length as well as the ratio of new to old trials. The order of trials on the implicit tests was randomized with the constraint that it began and ended with two filler pairs. For the study task, objects remained on the screen for 6000ms regardless of the timing of response, after which the next trial appeared automatically. For the implicit task, objects were cleared from the screen after the subject's response and were replaced with a fixation cross, which remained on the screen until the onset of the subsequent trial, with a consistent ISI of 4000ms.

### *Procedure*

For the encoding task in the same-cue block, subjects were told to view each trial and decide, by pressing the buttons labeled as “left” or “right” (the j and k keys) *which of the two presented objects was more likely to be found inside a house*. Subjects were asked to use their dominant hand to press both buttons. The encoding task was followed by a three-minute distractor task consisting of anagram puzzles. Subjects then completed the corresponding implicit test, in which they were asked again to decide which object was more likely to be found inside a house, as quickly as possible without sacrificing accuracy. Subjects were told that a fixation cross would appear after they key-pressed their response, and that they should keep their eyes focused on the cross, because the next trial would appear there and this would make it easier to respond quickly. For the reverse-cue block, the encoding procedure was identical to encoding in same-cue block. After a distractor task consisting of arithmetic problems, the reverse-cue implicit test asked subjects to decide which of the two objects was more likely to be found *outside* a house.

### *Results and Discussion*



Mean reaction times and standard deviations for each retrieval condition are displayed in Table 8. Outliers of more than two standard deviations from the mean were removed from each condition in each subject, and only correct responses were included in analyses. These procedures yielded 4.8% of trials excluded in young adults and 6.1% excluded in old adults. Like Experiment 4, older adults had slower baseline RTs than younger adults when collapsing across cue conditions, ( $t(62) = -6.69, p < .001$ ). Using a mixed ANOVA with same-cue and inverted-cue baseline (i.e., new trial) reaction times as a within-subjects factor and age as a between-subjects factor, there was not a significant overall effect of cue reversal on baseline reaction times ( $F(1, 62) = 1.55, p = .22$ ), nor was there a significant interaction between switch costs and age ( $F < 1$ ). Thus, unlike Experiment 4, there was no evidence of task switch costs in either age group. Although this presents a different pattern from Experiment 4, such mixed findings are not inconsistent with the prior literature: task switch costs are sometimes found (Schnyer et al., 2007, Exp. 1 block 2), and sometimes there is no baseline difference between same-cue and inverted-cue trials (Schnyer et al., 2007, Exp. 1 block 1). Baseline trials in both the same and inverted trials were slower for both age groups in Experiment 5 relative to the identical conditions in Experiment 4, possibly suggesting that the associative classification is more difficult than the item-level version.

Item priming was measured as RTs to baseline critical new trials minus RTs to recombined trials. Rapid response learning was measured as a priming reduction for the reverse-cue condition relative to the same-cue condition. As with the previous experiments, mean priming effects are listed in Table 10. Using a 3-way ANOVA with factors of age, item priming (recombined versus new) and cue condition (same versus reversed), there was a significant effect of item priming ( $F(1, 62) = 115.15, p < .001$ ), with reaction times faster for

recombined trials than new trials. There was also a significant effect of cue condition ( $F(1, 62) = 4.51, p < .05$ ), with overall reaction times in the reverse-cue condition slower than in the same-cue condition. There was a significant interaction between item priming and age ( $F(1, 62) = 7.34, p < .01$ ), with in fact more item priming in the older than young adults. This age difference is likely a function, at least in part, of the slower baseline reaction times in older adults; when priming was re-calculated as a function of percent change from baseline (i.e., rather than RT difference), there was only a marginally significant age difference ( $t(62) = 1.82, p = .07$ ), with 11.3% change in young adults and 17.4% change in older adults. Still, the finding of more item priming in the older adults was not eliminated when using the measure of percent change. Unlike Experiment 4, there was not a significant interaction between priming and cue condition ( $F(1, 62) = 1.53, p = .22$ ). This finding implies that a high degree of repetition specificity may be a necessary criterion for rapid response learning. Importantly, there was not a significant interaction between condition and age group ( $F < 1$ ), indicating that no age difference in the magnitude of task switch costs. Lastly, there was not a significant 3-way interaction between priming, cue condition, and age ( $F(1, 62) = 2.55, p = .12$ ), demonstrating that the effect of cue reversal on priming was not moderated by age.

Associative priming was measured as response times to recombined trials minus response times to intact trials. Using a 3-way ANOVA with factors of age, associative priming (intact versus recombined trials) and cue condition (same-cue versus reverse-cue trials), there was a significant overall effect of associative priming ( $F(1, 62) = 6.34, p = .01$ ), with faster reaction times to intact relative to recombined pairs. There was also a significant effect of condition, ( $F(1, 62) = 21.02, p < .001$ ), with overall RTs slower in the reverse-cue condition relative to the same-cue condition. There was no interaction between age and

associative priming ( $F < 1$ ), showing that both age groups encoded the novel association between the object pairs and were sensitive to the context change. There was an interaction between age and cue condition that approached significance, ( $F(1, 62) = 3.82, p = .056$ ), indicating that task switch costs for the studied trials (i.e., collapsed across intact and recombined) were relatively larger in older than younger adults. Importantly, there was a significant interaction between condition and associative priming, ( $F(1, 62) = 3.94, p = .05$ ), showing that cue reversal significantly reduced associative priming. Follow-up  $t$ -tests revealed that cue reversal in fact eliminated associative priming in both age groups: priming was significantly greater than zero in the same-cue condition in young ( $t(31) = 2.51, p < .05$ ) and older ( $t(31) = 2.55, p < .05$ ) adults, but was not significantly greater than zero in the reverse-cue condition in either young ( $p = .73$ ) or old ( $p = .64$ ) adults. Indeed, in the omnibus test, there was no 3-way interaction between condition, associative priming, and age ( $F < 1$ ), showing that the effect of cue reversal on associative priming was not modulated by age. Experiment 5 thus extended the pattern of response specificity to another type of stimulus-response learning, and can be seen as consistent with the difference between the re-pair match and re-pair mismatch conditions from Dennis and Schmidt (2003).

The pattern of equivalent associative priming in the same-cue condition replicates findings from Experiments 1 and 2, and shows that the older adults were able to form an associative link between unrelated objects as well as young adults under the incidental encoding condition. Importantly, inverting the decision cue disrupted associative priming to a similar extent in both age groups. It is therefore unlikely that the pattern of rapid response learning in Experiment 4 emerged only because of the simplicity of the paradigm. In contrast with prior findings in the literature in which age-related memory performance was disrupted

by an increased number of features (Gagnon et al., 2007; Mitchell et al., 2000a), older adults formed a stimulus-response link even when required to form an additional association between the object stimuli. Although one could argue that the lack of associative priming was not due to stimulus-response learning but rather reflected insufficient encoding of the association between the object stimuli, this possibility is unlikely. The encoding conditions were identical under both the same-cue and reversed-cue conditions, with the order of the blocks counterbalanced across subjects. It was only when the retrieval instructions were manipulated that priming was affected; therefore an encoding explanation is not tenable. Rather, the retrieval manipulation in Experiment 5 highlights stimulus-response learning as a mechanism underlying priming in this paradigm, consistent with recent interpretations of repetition priming (Dobbins et al., 2004; Horner & Henson, 2008, 2009; Schnyer et al., 2006, 2007).

Of note, the lack of age differences in associative priming and in rapid response learning presents an important difference between healthy aging and MTL-amnesia. For instance, while Schnyer et al. (2006) found that repetition priming in patients with MTL damage was unaffected by cue inversion, priming in the healthy older adults here was affected to the same extent as young adults. Although both populations have been described as having a deficit in associative processing, the impairments may have different sources. There has been some evidence that the medial temporal lobes are relatively unaffected by healthy aging, despite marked impairments in this region in conditions of pathological aging such as Alzheimer's Disease (e.g., Head, Snyder, Girton, Morris & Buckner, 2005). Instead, the associative deficit in older adults may stem from impairments in the prefrontal cortex (PFC) (Head et al., 2005), which is involved in the strategic organization or manipulation of

associative features (Buckner, 2003; Dobbins, Foley, Schacter & Wagner, 2002), or may stem from impairments in the circuitry between the PFC and the hippocampus (Li, Naveh-Benjamin & Lindenberger, 2005; Mitchell, Johnson, Raye & D'Esposito, 2000b). The effect of aging on the roles of MTL and PFC during associative memory is examined in detail in Experiment 6.

## CHAPTER XVI

### EXPERIMENT 6

Experiment 6 used fMRI to examine the neural basis of implicit and explicit associative memory in young and older adults. Experiment 6 had several goals, including distinct motivations and hypotheses for the two age groups. These goals are described in turn below, beginning with the young adults.

The first goal was to examine the role of MTL regions during implicit retrieval of new associations. As described previously, very little is known about the neural basis of implicit associative memory. However, fMRI studies to date converge with neuropsychological studies (Carlesimo et al., 2003; Ryan et al., 2000) that posit a special role of the MTL in associative memory at both explicit and implicit levels of awareness. Interestingly, the precise nature of MTL involvement in associative priming is currently controversial. While a study of unaware semantic associative retrieval observed *active* bilateral hippocampus and right perirhinal cortex (Henke et al., 2003), a study of unaware perceptual associative retrieval observed *deactivations* in right parahippocampal gyrus (Yang et al., 2008). Given these findings, Experiment 6 tested the possibility that the MTL is differentially engaged during conceptual versus perceptual associative priming.

The associative speeded classification task from Experiments 2, 3, and 5 was used to assess associative priming. Of note, using a standard (i.e., non-associative) speeded response paradigm in which subjects made size judgments, Koutstaal et al. (2001) directly compared conceptual and perceptual priming of pictured objects. Neural activity was compared for

repeated relative to novel trials (i.e., repeated conceptual judgment), as well as for repeated trials relative to trials with a different exemplar of the same object (i.e., a perceptual manipulation). Repeated relative to novel trials and repeated relative to different-exemplar trials were associated with reductions in neural activity in several of the same regions: bilateral inferior and superior frontal regions, parahippocampal gyrus, fusiform gyrus, precuneus, and posterior cingulate (see also Buckner et al., 1998, for similar findings).

In Experiment 6, priming for new conceptual associations was assessed as neural activity that was greater for recombined trials relative to intact trials. To examine perceptual associative priming, the trials were utilized the trials in which the colors of studied objects were recombined to create re-colored versions of otherwise intact trials (i.e., the *object-feature* relationships were manipulated). Perceptual associative priming was then assessed as neural activity that was greater for re-colored trials relative to intact trials. Based on findings from the speeded object classification task used by Koustaal et al. (2001) and Buckner et al. (1998), I predicted that both the conceptual and perceptual manipulations would be associated with repetition-related decreases in activity in a distributed network of neural regions, including frontal, fusiform, middle occipital, posterior cingulate cortex and precuneus. The critical question for present purposes concerned the role of the hippocampus and adjacent parahippocampal gyrus (PHG) given the *associative* component of the paradigm and comparisons. If different regions of the MTL are differentially involved in implicit retrieval of conceptual versus perceptual associations, then the hippocampus and PHG should show repetition-related *increases* in activity during conceptual associative priming (i.e., corresponding with Henke et al., 2003), but PHG *decreases* in activity during perceptual associative priming (i.e., corresponding with Yang et al., 2008).

The second goal of Experiment 6 was to compare associative priming with item priming. A limitation of comparing item and associative priming across different studies in the current literature is that item priming has typically involved the repetition of single stimuli, whereas associative priming typically involves two stimuli or a stimulus-feature relationship. As described previously, recombined pairs are comprised of repeated individual objects in the absence of a repeated association. Thus, activity that is greater for new relative to recombined trials can be taken as a measure of item priming. Importantly, this measure of item priming uses the same type of stimuli and encoding paradigm that are used to obtain estimates of associative priming. The use of the identical stimuli and retrieval manipulation to compare item and associative priming increases the validity of interpretations regarding differences in their neural bases. Based on Buckner et al. (1998) and Koutstaal et al. (2001), I predicted that item priming would be linked with deactivations in several neural regions including fusiform gyrus, occipital cortex, and superior and inferior frontal regions. However, unlike associative priming, I predicted that item priming would not engage the hippocampus.

The third goal of Experiment 6 was to compare associative priming with associative recognition. While relational binding processes have been linked to the MTL (Davachi, et al., 2003; Eichenbaum, et al, 2000; Giovanello, et al., 2004) explicit relational retrieval has been linked to both the MTL and the PFC, to the extent that explicit retrieval also involves an intentional or strategic attempt to remember associative information (Buckner, 2003; Dobbins, et al., 2002; Velanova et al., 2003). As such, I hypothesized that the distribution of activations and deactivations during implicit retrieval would differ from the neural basis of explicit relational retrieval, during which I expected increased activity in the hippocampus as



well as the prefrontal cortex (e.g., Buckner & Wheeler, 2001; Kim & Cabeza, 2009; Rudy, Biedenkapp & O'Reilly, 2005; Schacter & Buckner, 1998a; Schendan, Searl, Melrose & Stern, 2003).

Lastly, in addition to the questions examined in young adults, the fourth goal of Experiment 6 was to determine the effects of aging on the neural basis of implicit and explicit relational memory. As described previously, the MTL is critical for associative processing even under nonconscious conditions (Carlesimo et al., 2003; Chun & Phelps, 1999; Henke et al., 2003; Ryan et al., 2000; Yang et al., 2008). There is evidence that the medial temporal lobes are relatively unaffected by healthy aging, compared with regions of more substantial change such as the prefrontal cortex (PFC) (Head, Snyder, Girton, Morris, & Buckner, 2005). On tasks that likely involve the MTL but not the PFC, such as spatial and contextual learning tasks that do not involve elaborative or strategic encoding, healthy older adults perform as well as young adults (Howard, Howard, Dennis, LaVine & Valentino, 2008; Howard, Howard, Dennis, Yankovich & Vaidya, 2004). The finding of preserved incidental associative processing seen in Experiments 1-5 thus fit well with this literature. An important question is whether the behavioral priming effect is associated with the same pattern of medial temporal lobe activity in the two age groups.

Experiment 6 thus investigated whether older and younger adults would show a similar or different pattern of neural activity during implicit relational retrieval, using a task on which behavioral equivalence was expected, given the findings in Experiments 1, 2, and 5. This study documents the first fMRI analysis of implicit associative memory in older adults, coupled with a within-subjects comparison with explicit associative memory that followed the same encoding manipulation. Based on prior studies of explicit item

(Giovanello et al., 2004; Gutchess et al., 2005; Grady et al., 2005) and relational (Giovanello et al., 2009) retrieval tasks that engaged both MTL and PFC regions in young adults, I predicted that age-related explicit associative recognition deficits would be associated with MTL dysfunction coupled with increased engagement of frontal regions. The critical question regarded the neural basis of behavioral age-equivalence during implicit relational retrieval. This experiment tested whether older and younger adults would: 1) show a similar pattern of MTL activity during a task that was independent from strategic retrieval processes; 2) whether aging would be associated with additional recruitment of frontal regions during associative priming that are not observed in young adults.

## Method

### *Participants*

Fourteen healthy young adults (4 male, ages 18-31,  $m = 20.8$ ; mean education = 14.5 years,  $sd = 2.10$ ) and fifteen healthy community-dwelling older adults (8 male, ages 61-88,  $m = 73.9$ ; mean education = 17.7 years,  $sd = 2.87$ ) with normal or corrected-to-normal vision participated in the experiment after providing informed written consent. Screening for MR safety took place at the time of recruitment and again on the day of scanning. Four older adult participants were excluded; one due to problems understanding the associative recognition task instructions, two due to structural outliers, and one due to a technical glitch with the MR response box during explicit retrieval. All participants were right-handed Native English speakers with no history of neurological or psychiatric conditions. Participants received \$20 per hour to compensate their time. No subjects in Experiment 6 had participated in Experiments 1-5.

### *Materials and behavioral procedure*

Experiment 6 was identical to Experiment 2, with the following modifications. First: the new trials were removed from the associative recognition task, such that only intact and recombined trials were included. The new trials were removed in order to improve accuracy and increase the number of correct rejection trials that could be modeled as events in the fMRI analyses. Second: control (i.e., null) trials were added to each experimental task and comprised one-third of the total trials in each run. These control trials are used to assess baseline activation levels. Trials consisted of two meaningful symbols (a dollar sign and a cents sign) presented in the same spatial locations as the two objects in each experimental trial, and subjects were instructed to decide on which side of the screen the dollar sign appeared. A randomized jittered ISI for control trials were variants of the ISI for experimental trials and ranged from 3000, 6000, or 9000ms. These jittered ISIs are implemented in order to increase the power to detect hemodynamic response differences that are specific to individual trial events. The program OptSeq (<http://surfer.nm.mgh.harvard.edu/optseq>) was used to determine the list order for each experimental and control trial that should optimally assess event-related activation.

Before entering the scanner, subjects completed a practice version of the first encoding task which consisted of 10 psuedo-experimental trials (not included in any analysis) and 3 control trials. Following a localizer and structural T1-weighted scan, subjects completed all four experimental tasks took inside the scanner. Subjects recorded all task responses by pressing a button on an MR-compatible response box using the index or middle finger of their dominant (right) hand. To allow the subjects to rest briefly during the experiment, a second T1-weighted anatomical scan was completed between the implicit test and the second encoding task and lasted approximately 7 minutes.

### *Image Acquisition and Analysis*

Subjects were scanned with a Siemens 3 Tesla head-only imaging system equipped for echo planar imaging (EPI; Siemens Medical Systems, Iselin, NJ), using a 3 axis gradient head coil. Stimuli were presented onto a screen and viewed through a mirror placed above the participant's head. Responses were recorded via response box using the dominant (right) hand. Head motion was restricted with a pillow and foam inserts. After automated scout and shimming procedures to optimize field homogeneity, one high-resolution T1-weighted MP-RAGE sequence with an in-plane resolution of 1.2 mm and 1.2 mm slice thickness was acquired (TR = 7.25 msec, TE = 3 msec, flip angle = 7 deg) to assist in the registration of the functional data to the high-resolution anatomical scans, along with brief sagittal localizer scan. Forty-six oblique coronal slices (3 mm thick, with 1 mm skip between slices; slices oriented along the long axis of the hippocampus, providing whole brain coverage extending from occipital to frontal poles) were positioned on the sagittal localizer. Functional MRI images were acquired using a gradient echo T2\*-weighted sequence in-plane resolution 3.125 mm, with a TR of 3000ms, TE 23 msec, flip angle 90 degrees, FOV read 192, FOV phase 100, and voxel dimensions = 3.125 x 3.125 x 6.0mm. The two initial TRs were acquired and discarded to allow the scanner to reach equilibrium.

Imaging data were preprocessed using SPM5 (Wellcome Department of Cognitive Neurology, London). Functional images were corrected for offsets in the time of acquisition by resampling all slices to match the first slice, which was used as a reference slice of the volume. Following this step, images were realigned and unwarped to correct for motion across runs and then spatially normalized to an EPI template normalized in MNI stereotactic space, using both a 12-parameter affine transformation and a nonlinear transformation using

cosine basis functions. Next, functional and anatomical images for each subject were co-registered to each other. Finally, the images were re-sampled into 3 mm cubic voxels and spatially smoothed with an 8mm full-width half-maximum Gaussian kernel and rescaled to a mean signal value of 100. Statistical analyses were performed using the general linear model for event-related designs in SPM8. For each participant, a whole-brain voxelwise analysis was conducted in which, individual events were modeled as a canonical hemodynamic response. Each event type was first modeled for each subject using a fixed effects analysis. These data were then entered into a between-subjects random effects analysis. The resulting least squares parameter estimates of the height of the modeled hemodynamic response for each condition were used in pairwise contrasts of interest, and were examined for significance at a threshold of  $p < .005$  (using an cluster extent threshold of  $k > 5$  contiguous voxels). If hypothesized cortical regions did not show significant clusters of activation at this threshold, I lowered the threshold to  $p < .05$  in order to determine whether hypothesized regions were active at the more lenient significance level. This more lenient threshold was applied only for hypothesis-driven analyses, and a larger extent threshold for contiguous voxel clusters ( $k > 10$ ) was concurrently applied (typical event-related fMRI studies use a cluster extent threshold of 3-5, see Huettel, Song & McCarthy, 2003). Conjunction analyses were conducted using the masking function in SPM8, and examined what regions were commonly activated by young and older adults. The threshold for each group's contrast entered into the analysis was set at  $p < .07$  ( $k > 5$ ) so that the conjoint probability using Fisher's estimate would be  $p < .005$  (Fisher, 1950).

The voxelwise analyses were followed by regions-of-interest (ROI) analyses in targeted significant regions in order to determine the pattern of activity in those regions. The

Wake Forest University PickAtlas software (<http://fmri.wfubmc.edu/cms/software>) was used to identify anatomically-defined regions of interest (ROIs), which were uploaded as masks into SPM8 using the Rex tool in order to extract  $\beta$  weights (parameter estimates) for each critical condition, which were averaged across subjects.

All activations are presented according to neurological convention, such that activity in the right hemisphere is presented on the right side of the brain image. Statistically significant activity is projected onto a canonical single-subject T1 structural image template. Voxel coordinates are reported according to Montreal Neurological Institute (MNI) space and represent the most significant voxel within the cluster.

Because the focus of analysis for the implicit data was repetition-related deactivations, neural activity associated with item (i.e., non-associative) priming on the speeded object classification task was examined by contrasting new trials > recombined trials. Repetition-related deactivations for conceptual associative priming was examined by contrasting recombined > intact trials. Because Henke et al. (2003) found repetition-related *increases* in bilateral hippocampus and PHG, I also contrasted intact > recombined trials to determine whether any MTL regions were more active for intact relative to recombined trials. Repetition-related deactivations for perceptual associative priming were examined by contrasting re-colored > intact trials. For the purpose of comparing with conceptual associative priming, I also contrasted the reverse, intact > re-colored trials, to determine whether any MTL regions were more active during intact than re-colored trials.

The neural correlates of explicit retrieval success are typically measured by comparing correctly identified old items (or old pairs) relative to correctly identified new items (or new pairs) (e.g., Rugg et al., 2002; Rugg & Wilding, 2000). As such, correctness of

response was held constant, yielding the contrast of correct responses to intact pairs (hits) minus correct responses to recombined pairs (correct rejections). Because older adults have demonstrated additional frontal activations during explicit relational retrieval (Giovanello et al., 2009a) and additional frontal deactivations during implicit item retrieval (Bergerbest et al., 2009), I further examined whether older adults recruited frontal regions above and beyond those recruited by young adults for each contrast of interest at  $p < .005$  ( $k > 5$ ).

## Results

### *Behavioral Data*

For the implicit speeded classification test, reaction times were compared among the four retrieval conditions (i.e., intact, recombined, new and re-colored). Mean reaction times and standard deviations for each age group are included in Table 9. As with the previous experiments, priming effects are listed in Table 10. Outliers of more than  $\pm 2$  standard deviations from the mean were removed from each condition in each subject. This procedure resulted in the exclusion of 2.3% of total trials from both behavioral and fMRI analyses. Using a mixed ANOVA with retrieval trial type as a within-subjects factor and age group as a between-subjects factor, there was a significant main effect of trial type ( $F(3, 69) = 33.93$ ,  $p < .001$ ), indicating that reaction times varied as a function of retrieval condition. There was no interaction between condition and age group,  $F < 1$ , indicating that the differences among trial types were not moderated by age. Planned follow-up contrasts revealed significant item priming, with faster reaction times to recombined pairs relative to new pairs in young ( $t(13) = -5.8$ ,  $p < .001$ ) and older ( $t(10) = -3.16$ ,  $p = .01$ ) adults. There was no difference in magnitude of item priming between the age groups,  $p = .85$ . Associative priming was also significant in young adults, with faster reaction times to intact pairs relative to recombined pairs, ( $t(13) = -$

2.5,  $p < .05$ ). Associative priming approached significance in older adults ( $t(10) = -2.14$ ,  $p = .067$ ) adults. The difference between intact and recombined pairs in older adults would likely have reached significance with a larger sample; indeed, when the implicit behavioral data were included from the 4 subjects whose neuroimaging data were excluded, associative priming was significant in older adults, ( $t(14) = 2.46$ ,  $p < .05$ ). Furthermore, although when the age groups were tested individually, the young but not older adults' associative priming crossed the threshold for statistical significance at  $p < .05$ , there was not a significant difference in associative priming between the age groups,  $p = .78$ . There was no difference between intact and re-colored pairs in young ( $p = .43$ ) or old ( $p = .86$ ), supporting the interpretation that the speeded object classification task is more sensitive to the overlap in conceptual-decision rather than perceptual cognitive operations.

Associative recognition accuracy in the behavioral measure was defined as hits to intact pairs minus false alarms to recombined pairs. In young adults, mean hit rate was .81 and mean false alarm rate was .47, yielding a mean accuracy rate of .34. In older adults, mean hit rate was .80 and mean false alarm rate was .66, yielding a mean accuracy rate of .14. Accuracy was significantly greater than floor in young ( $t(13) = 8.4$ ,  $p < .001$ ) and older ( $t(10) = 2.7$ ,  $p < .05$ ) adults, with accuracy significantly greater in the young relative to old ( $t(24) = 3.60$ ,  $p = .001$ ).

### *Imaging results*

The results of the fMRI analyses are described as a function of each research question of interest. These results are also listed systematically in table format. For all primary questions, regions of significance from the whole-brain voxelwise analysis in young adults are listed in Table 11 and in older adults are listed in Table 12. Regions commonly activated



by both age groups are listed in Table 13. Regions more activated in young than old are listed in Table 14, and regions more activated in old than young are in Table 15. Hypothesized medial temporal regions associated with conceptual and perceptual associative priming are listed in Table 16. Hypothesized regions associated with explicit recognition are listed in Table 17. Regions of additional frontal recruitment in older adults are listed in Table 18.

*Neural regions associated with conceptual associative priming*

I contrasted activity for recombined trials greater than intact trials to determine conceptual associative priming. In young adults: this contrast revealed activity in left inferior frontal gyrus (BA 44/47), bilateral middle frontal gyrus (BA 6/9); left middle occipital gyrus (BA 19); left middle and superior temporal gyrus (BA 21/22) and the right insula. In older adults: this contrast yielded activity in left inferior frontal gyrus (BA 45), bilateral middle and superior frontal gyrus (BA 9/10/11), right middle temporal gyrus (BA 29), right posterior cingulate (BA 29), bilateral precuneus (BA 7/31), and right superior parietal lobule (BA 7). To determine whether any medial temporal regions demonstrated repetition-related deactivations, I contrasted recombined>intact trials at  $p<.05$ . Of note, no medial temporal regions showed significant clusters of activity at this more lenient threshold in either age group. In addition to testing the age groups separately, I ran a conjunction analysis to determine regions of common activation. This analysis yielded significant activity in bilateral inferior frontal gyrus (BA 44), right posterior cingulate (BA 29), right inferior parietal lobule (BA 40), and right insula (BA 13). Lastly, I conducted a between-groups analysis to determine regions that were more active in young than old, and more active in old than young, for the recombined>intact contrast. Young adults showed more repetition-related deactivations than old in several frontal regions, including left inferior frontal gyrus (BA 47),

bilateral middle and superior frontal gyrus (BA 6/10/11), and left middle temporal gyrus. In contrast, older adults showed more deactivations than young in several parietal and occipital regions, including bilateral fusiform gyrus (BA 20/37), superior occipital gyrus (BA 19), bilateral cingulate gyrus (BA 30/24/32), left cuneus (BA 7/19), right precuneus (BA 7), bilateral insula (BA 13), and bilateral lingual gyrus, as well as left middle frontal gyrus (BA 10).

*Neural regions associated with hypothesized increases in activity during conceptual associative priming*

In addition to the repetition-related deactivations assessed by recombined>intact, I held two hypotheses regarding repetition-related *increases* during conceptual associative priming, assessed by intact>recombined trials. In regards to this contrast, I report here only the results of the hypothesis-driven analysis. First, I hypothesized that MTL regions would be involved in repetition-related increases in both age groups. In young adults: the contrast revealed significant activity in bilateral hippocampus, right entorhinal cortex on the parahippocampal gyrus (BA 28), and left parahippocampal cortex (BA 36). In older adults: this contrast revealed significant activity in left hippocampus and right entorhinal cortex on the PHG (BA 28). Common to both young and older adults was activity in left hippocampus and right entorhinal cortex (BA 28). Parameter estimates for hypothesized MTL regions during conceptual associative priming are graphed in Figure 1. Second, I hypothesized that aging would be associated with over-recruitment of anterior regions during conceptual associative priming. Several frontal regions were more active in older adults than younger adults, including bilateral middle frontal gyrus (BA 10/11), left inferior frontal gyrus (BA 47), and right dorsolateral PFC (BA 9). The neural regions more activated by older than

young adults in this contrast as well as the parameter estimates for right dorsolateral PFC (in BA 9) during intact and recombined trials are represented in Figure 2.

*Neural regions associated with perceptual associative priming*

We contrasted activity for re-colored trials greater than intact trials to determine perceptual associative priming. In young adults: this contrast revealed activity in bilateral middle frontal gyrus (BA 8/9), right superior frontal gyrus (BA 6); bilateral inferior frontal gyrus (BA 47); right superior parietal lobule (BA 7), bilateral inferior temporal gyrus (BA 20/21); right middle occipital gyrus (BA 19), bilateral putamen, left amygdale, and right cingulate gyrus. Notably, significant activity was seen in left perirhinal cortex on the parahippocampal gyrus (BA 35). In older adults: this contrast yielded activity in several temporal and occipital areas, including bilateral cingulate gyrus (BA 23/31), left cuneus (BA 19), bilateral precuneus (BA 31/39), bilateral insula (BA 13), right middle occipital gyrus (BA 19/39), bilateral postcentral gyrus (BA 23/40), right precentral gyrus (BA 6), and right superior temporal gyrus (BA 22/13). Common to both young and older adults was activity in several regions, including medial temporal regions (left hippocampus and bilateral entorhinal cortex in BA 28), parietal regions (right cuneus, bilateral precuneus, right angular gyrus in BA 39, bilateral superior temporal gyrus in BA 22/39, middle temporal gyrus in BA 39,) right middle occipital gyrus (BA18/19), and bilateral posterior cingulate. In the between-subjects analysis, young adults showed more repetition-related deactivations than older adults in several frontal regions, including right dorsolateral PFC (BA 6/8/9), bilateral middle frontal gyrus (BA 6/9/11), left inferior frontal gyrus (BA 47), as well as right inferior and superior parietal lobule (BA 7/40). Older adults showed more repetition-related deactivations than young adults in several temporal and occipital regions, including left cuneus (BA 18/19),

right inferior and middle occipital gyrus (BA 19), bilateral insula (BA 13), superior temporal gyrus (BA 22), as well as right entorhinal cortex (BA 28) and parahippocampal cortex (BA 36). Lastly, to determine whether any additional hypothesized MTL regions were associated with perceptual associative priming, I contrasted re-colored>intact trials at  $p < .05$  ( $k > 10$ ). In young adults, in addition to left perirhinal cortex on the PHG (listed previously at  $p < .005$ ), this contrast yielded activity in left hippocampus, and right entorhinal cortex on the PHG. In older adults, this contrast yielded activity in left entorhinal cortex (BA 34) and right perirhinal cortex (BA 35). Parameter estimates for hypothesized MTL regions during perceptual associative priming are graphed in Figure 2.

*Neural regions associated with increases in activity during perceptual associative priming*

In contrast to our hypothesis that MTL regions would be involved in repetition-related increases (rather than decreases) during conceptual associative priming, I hypothesized that no MTL regions would be increased during perceptual associative priming. To examine this hypothesis, I contrasted activity that was greater for intact than re-colored trials and report here only the results of the hypothesis-driven analysis. Consistent with our hypothesis, no MTL regions were activated, even at a lenient threshold of  $p < .05$ . Second, I hypothesized that, like conceptual associative priming, perceptual associative priming would also be associated with more repetition-related increases in frontal regions in older adults than young adults. This comparison yielded significant activity in left inferior frontal gyrus (BA 47), and left middle frontal gyrus (BA 9/11) and right dorsolateral PFC (BA 9). The neural regions more activated by older than young adults in this contrast as well as the parameter estimates for right dorsolateral PFC (in BA 9) during intact and re-colored trials are represented in Figure 4.

### *Neural regions associated with item priming*

To examine item priming, I contrasted activity that was greater for new than recombined trials. In young adults: this contrast revealed activity in bilateral associative visual cortex (BA 19); bilateral precentral gyrus (BA 4/6); right postcentral gyrus (BA 2/40); right precuneus (BA 7); bilateral superior temporal gyrus (BA 22/41); left middle temporal gyrus (BA 21); bilateral inferior temporal gyrus (BA 20) bilateral middle frontal gyrus (BA 6/10); left insula, and left anterior cingulate gyrus (BA 24). No medial temporal regions were activated at this level of significance, or at a more lenient threshold of  $p < .05$ . In older adults: this contrast yielded activity in right middle frontal gyrus (BA 11), right precentral gyrus (BA 6) and left postcentral gyrus (BA 43). Like the young adults, older adults did not show any significant MTL regions, even at  $p < .05$ . Regions of activation common to young and older adults included bilateral cingulate gyrus, right fusiform gyrus, bilateral superior and middle temporal gyrus (BA 21), bilateral postcentral gyrus (BA 3/40), bilateral precentral gyrus (BA 4/6), bilateral superior frontal gyrus (BA 6/9/10), and left superior parietal lobule (BA 7). The between-groups analysis showed that young adults produced more item-repetition-related deactivations in bilateral cingulate gyrus (BA 24/30), left fusiform gyrus (BA 37), right inferior frontal gyrus (BA 46), right inferior temporal gyrus (BA 20), bilateral middle frontal gyrus (BA 6/9), left precentral gyrus (BA 6), and left precuneus (BA 7). Older adults showed more deactivation than young adults in only one region: superior temporal gyrus (BA 22).

### *Neural regions associated with increases in activity during item priming*

Like associative priming, I hypothesized that repetition-related increases during item priming would be observed in frontal regions in older adults compared with young adults. To

examine this hypothesis, I contrasted activity that was greater for recombined trials than new trials and report only the results of the hypothesis-driven analysis. Older adults showed significantly greater activity than young adults in right inferior frontal gyrus (BA 46) and right dorsolateral PFC (BA 9).

*Neural regions associated with successful explicit associative retrieval*

Successful explicit relational retrieval was assessed by correct responses to intact trials (hits)>correct responses to recombined trials (correct rejections). In young adults: this contrast revealed activity in right superior temporal gyrus (BA 22), right inferior frontal gyrus (BA 11), right precuneus (BA 7), and left inferior frontal gyrus (BA 47). To determine whether additional hypothesized regions based on prior studies of explicit relational retrieval would be activated at a lower threshold, I contrasted hits>correct rejection at  $p < .05$  ( $k > 10$ ). These include: bilateral inferior parietal lobule (BA 40), right fusiform gyrus (BA 37), right middle frontal gyrus (BA 9/46), and right hippocampus. In older adults: activity significant at  $p < .005$  ( $k > 5$ ) was found in left precentral gyrus (BA 6). At  $p < .05$  ( $k > 10$ ), significant activity was found in bilateral precuneus (BA 7), bilateral inferior parietal lobule (BA 40), and bilateral inferior and middle frontal gyrus (BA 11/40). The conjunction analysis showed that the only region of common activity for young and older adults was the left cingulate gyrus. The between-subjects analysis showed that young adults yielded more activity than older adults in a variety of frontal, parietal, and temporal regions, including bilateral inferior frontal gyrus (BA 13/47), right middle frontal gyrus (Ba 11/21), right cingulate gyrus (BA 24/31), right superior temporal gyrus (BA 22/38/39), right precentral gyrus (BA 19), right fusiform gyrus (BA 20), right cuneus (BA 7), and and bilateral precuneus (BA 7/19). In contrast, older adults showed more activity than young adults in left middle and inferior

frontal gyrus (BA 10/45), left anterior cingulate (BA 32), left superior parietal lobule (BA 7), left cingulate gyrus (BA 31), and left precentral gyrus (BA 6).

### *Correlational analyses*

Across the three priming comparisons, the most consistent specific region of increased frontal activation in older adults was in right dorsolateral PFC (BA 9). To assess the hypothesis that increased activity in this region was associated with conceptual and perceptual associative priming performance, I extracted parameter estimates of mean activation levels in this region during each memory condition using anatomically-defined regions-of-interest (ROI) analyses. I then correlated the mean activation levels in right BA 9 during the intact condition with intact reaction times using Pearson's correlation. This correlation was significant,  $r = -.53$ ,  $p < .05$  (one-tailed), showing that more activity was associated with faster reaction times. In contrast, there was no relationship between activity in this region and intact RTs in young adults ( $p = .39$ ). Next, I correlated the mean activation level in right BA 9 during the re-colored trials with re-colored reaction times. In older adults, there was a negative correlation that was nearly significant ( $r = -.51$ ,  $p = .056$ ), showing that activity in this region during re-colored trials was generally associated with faster reaction times. In contrast, there was no significant relationship between activity in this region and re-colored RTs in young adults ( $p = .12$ ). I also correlated the mean activation level in right BA 9 during the recombined condition with recombined reaction times to determine if activity in this region was associated with item priming performance in older adults. This correlation was nearly significant ( $r = -.50$ ,  $p = .059$ ) showing that increased activity in this region was generally associated with faster RTs to recombined trials. In contrast, again, there was no association between activity in this region and recombined RTs in young adults ( $p = .43$ ). To

determine whether these significant correlations in older adults reflected an association between right BA 9 activation and a generalized ability on reaction time tasks rather than with *priming* specifically, I also correlated activity in right BA 9 during new trials with new RTs. There was no relationship in young ( $p = .19$ ) or older adults ( $p = .45$ ). No other frontal regions significantly correlated with reaction times in any retrieval condition (all  $ps > .1$ ). However, there was a positive relationship between activity in right BA 9 and right hippocampus during intact trials that approached significance ( $r = .48$ ,  $p = .06$ ) in older adults. There was no relationship between these regions in young adults, ( $r = -0.007$ ,  $p = .49$ ).

Lastly, to determine whether the increases in left anterior PFC (BA 10) seen during explicit retrieval were associated with behavioral performance, mean activity level in left BA 10 during correct rejection trials was correlated with mean proportion of correct rejections (which was more reflective of variance in behavioral performance than hit rate, which was largely similar across OAs and between OAs and YAs). This correlation was not significant in young ( $p = .14$ ) or old adults ( $p = .31$ ).

## Discussion

Experiment 6 used event-related fMRI to examine conceptual and perceptual associative priming, item priming, and associative recognition, all of which followed the identical encoding manipulation. Because distinct motivations and hypotheses were held for each age group, the young and older adult findings are discussed separately.

### *Young Adults*



In regards to conceptual associative priming, Experiment 6 utilized an associative version of a standard speeded classification task which, in Experiment 3, was shown to be functionally independent from explicit retrieval. Based on prior studies of unaware semantic associative retrieval (e.g., Degonda et al., 2005; Henke et al., 2003), the primary interest was in whether the MTL, and specifically the hippocampus, would show more activity during repeated relative to recombined pairs. To examine this specific hypothesis, I used a lenient threshold of  $p < .05$  ( $k > 10$ ) and observed significant clusters of activity in bilateral hippocampus, right entorhinal cortex and left parahippocampal gyrus during implicit retrieval of novel conceptual associations.). Of note, when this contrast was reversed to examine which regions were associated with repetition-related *deactivations*, no MTL regions were observed. The finding of greater hippocampal activity to intact pair trials relative to recombined pair trials is consistent with several prior studies in the neuropsychological (Carlesimo, et al., 2005; Chun & Phelps, 2000; Park, et al., 2004; Ryan et al., 2000) and fMRI (Degonda et al., 2005; Hanuula & Ranganath, 2009; Henke et al., 2003; Schendan et al., 2003) literatures that posit a contribution of the hippocampus to relational memory, regardless of whether memory is assessed directly (i.e., using tests of explicit memory) or indirectly (i.e., using tests of implicit memory).

This Experiment also examined the role of the hippocampus in implicit memory for new non-semantic (i.e., perceptual) associations. Critically, Yang et al. (2008) found that perceptual priming of unrelated word pairs was associated with decreased activity in parahippocampal gyrus (PHG), but not the hippocampus. To examine whether MTL regions would be associated with deactivations during perceptual associative priming in our study, the colors (i.e., a perceptual feature) of the studied objects were recombined, which allowed

for the assessment of activity that was more greater during re-colored than intact pairs. There were significant clusters of activity in left hippocampus, right entorhinal cortex, and left PHG. Thus, producing the opposite direction from conceptual associative priming, these regions were associated with repetition-related *deactivations*. Importantly, no MTL regions were more active during intact than re-colored trials. The negative direction of neural response in MTL during perceptual associative priming is consistent with the deactivations during unaware perceptual associative retrieval reported by Yang et al. (2008). The fact that the present study observed the same direction of response as Yang et al. during priming of new perceptual associations is consistent with my hypothesis that the nature of the association may explain the divergent findings between Yang et al. (2008) and Henke et al. (2003). More generally, these collective findings suggest a functional dissociation within the medial temporal lobes during implicit retrieval of conceptual and perceptual associations. Further data are needed to determine the generality of the present findings and the types of perceptual representations for which the hippocampus is sensitive.

It is uncertain what precisely accounts for the differential direction of MTL activity between conceptual and perceptual associative priming. One possibility is that they differ along the criterion of relational versus conjunctive binding (see Cohen & Eichenbaum, 1993; Cohen et al., 1997; Mayes et al., 2007). Relational representations are flexible, such that the binding of components A, B, and C can later be accessed as any variation of the original inputs, including (for instance) AB, AC, BC, or ABC. Conversely, conjunctive representations become merged, such that binding of components A, B, and C can later be accessed only as the fused ABC. The neural basis of relational versus conjunctive representations is still uncertain (Moses & Ryann, 2006), although the distinction between

relational and conjunctive binding has recently been used as an analogue to the distinction between recollection- and familiarity-based explicit memory (for a review see Mayes et al., 2007). Of note, the direction of activity for recollection and familiarity converges with the respective directions of conceptual and perceptual associative priming in the present experiment: While recollection has been linked with increases in activity (e.g., Davachi & Wagner, 2002; Ranganath et al., 2004), familiarity has been linked with deactivations (e.g. Daselaar et al., 2006; Gonzalves et al., 2005; Henson et al., 2003). The present experiment did not systematically operationalize relational versus conjunctive binding, but it might be reasonable to conjecture that object-object associations map more strongly onto a relational representation, whereas object-feature associations map more strongly onto a fused, conjunctive representation. At the very least, this possibility points to the effect of relational versus conjunctive binding on implicit memory as an important avenue of future research.

One critical difference between the present findings and those reported by Yang et al. (2008) concerns the role of the hippocampus in particular during perceptual associative priming. While the current study found deactivations in the left hippocampus, as well as right entorhinal cortex and left PHG, Yang et al. found deactivations in parahippocampal gyrus, but did not observe any hippocampal involvement. There are several interesting possibilities that could account for why I obtained a different result from Yang et al. (2008). One possibility is that the reading measure used by Yang and colleagues could have been sensitive to trials in which the characters had been perceived as a cohesive unit, rather than as associations per se. Indeed, PHG deactivations are not unique to associative priming; repetition-related deactivations have been found in PHG during repetition of single objects (e.g., Buckner et al., 1998; Koutstaal et al., 2001). There is also evidence that if associative

pairs become unitized, activity is observed in perirhinal cortex (the anterior portion of the PHG) (Haskins, Yonelinas, Quamme & Ranganath, 2008). This region sometimes shows *deactivations* during familiarity-based recognition (Daselaar, Fleck & Cabeza, 2006; Gonsalves et al., 2005; Henson et al., 2003; Montaldi et al., 2006), perhaps as function of perceptual fluency (Haskins, et al., 2008), and has been shown to be more involved in item than relational memory (Giovanello et al., 2004). A second possibility for why the present experiment obtained a different result from Yang et al. (2008) is that the conjunctive measure of associative retrieval used in their study (i.e., the overlap between old>recombined and old>new) may have conflated associative processing with item processing, thereby masking hippocampal involvement. Lastly, a third possibility concerns the difference in the threshold of significance between the present study and the one used by Yang et al. (2008). Because hippocampal deactivations were revealed in the present study only when the threshold for statistical significance was lowered, it is possible that Yang et al. (2008) could have observed hippocampal deactivations at a similar threshold. Indeed, in that study, activity is reported only at the stricter level of  $p < .001$ . The alternative possibility that the involvement of the hippocampus seen in the present study actually resulted from explicit processing is not tenable, given the direction of activity.

In addition to the hypotheses regarding MTL regions, I also hypothesized that both conceptual and perceptual associative priming would involve decreases in activity in non-MTL regions. These deactivations were examined by contrasting activity that was greater for recombined trials than intact trials (for conceptual associative priming) and activity that was greater for re-colored than intact trials (for perceptual associative priming). The non-MTL regions activated in these comparisons were consistent with hypothesized regions based on

the speeded object classification task used by Koutstaal et al. (2001) and Buckner et al. (1998). These included several regions within frontal cortex, specifically inferior frontal gyrus (corresponding to BA 47), dorsolateral prefrontal cortex (corresponding to BA 9) and superior frontal gyrus/premotor cortex (corresponding to BA 6). Deactivations in these frontal regions possibly reflect greater efficiency in classification decision processes during the experimental paradigm or in stimulus-response mapping (consistent with neural priming effects in frontal gyrus, e.g., Dobbins et al. 2004), as well as greater facilitation in motor-response operations. Repetition-related deactivations were observed in visual processing areas including middle occipital gyrus (corresponding to BA 19), possibly reflecting increased ease in object identification. Unlike perceptual associative priming, conceptual associative priming was additionally linked with deactivations in inferior BA 44 (corresponding to Broca's area), which are often observed during conceptual priming (e.g., Wagner et al., 1997), mostly likely due to this region's involvement in language processing. Conceptual and perceptual associative priming differed to some degree in hemispheric engagement, with conceptual associative priming involving primarily left-lateralized areas and perceptual-associative priming involving primarily bilateral areas. Left-lateralized activation is typical of amodal conceptual priming (Meister et al., 2005; Wagner et al., 1997). Right-lateralized or bilateral deactivations have been shown to occur during priming of nameable picture stimuli (Bunzeck, Schutze & Duzel, 2006; Koutstaal et al., 2001). Bilateral involvement in the present study during perceptual associative priming is thus not unexpected given this comparison's manipulation of surface-level features.

In addition to associative priming, our paradigm also yielded a measure of item priming. The comparison of new greater-than recombined trials yielded significant activity in

several of the same neural regions as was found during perceptual and conceptual associative priming, including bilateral inferior temporal gyrus, bilateral middle occipital cortex, bilateral medial frontal gyrus, and bilateral cingulate gyrus. This network of deactivations are consistent with the deactivations found by Koutstaal et al. (2001) and Buckner et al. (1998) during speeded object size classification. Similar to associative priming, these repetition-related deactivations possibly reflect the facilitation in multiple cognitive processes operative in the classification task, including visual object perception and classification decision processes. Critically, in contrast to conceptual and perceptual associative priming, item priming in the current study did not involve any MTL regions. To determine whether the lack of MTL involvement could have been a function of Type II error, such that potentially real differences did not pass the threshold of significance at  $p < .005$ , the threshold was lowered to a lenient level of  $p < .05$ . No MTL activity was observed at this level. Importantly, this finding dissociates item priming from associative priming in regards to the involvement of the medial temporal lobes, consistent with the neuropsychological literature (Carlesimo, et al., 2005; Chun & Phelps, 2000; Park, et al., 2004; Ryan et al., 2000) that has shown preserved item priming in the context of impaired associative priming for patients with damage to the medial temporal lobes.

Finally, explicit, associative recognition followed implicit testing and a second, otherwise identical incidental encoding manipulation. A critical feature of this design is that differences in explicit and implicit retrieval cannot be explained by differential encoding operations. The neural correlates of explicit retrieval success are typically measured by comparing correctly identified old items relative to correctly identified new items (e.g., Rugg et al., 2002; Rugg & Wilding, 2000). As such, correctness of response was held constant,

yielding the contrast of correct responses to intact pairs (hits) minus correct responses to recombined pairs (correct rejections). The regions involved in successful explicit relational retrieval were consistent with findings in prior studies (e.g., Buckner & Wheeler, 2001; Giovanello et al., 2009b; Kim & Cabeza, 2009; Prince et al., 2005; Rudy, Biedenkapp & O'Reilly, 2005; Schacter & Buckner, 1998a; Schendan, Searl, Melrose & Stern, 2003). These included several frontal regions including bilateral inferior frontal gyrus and right middle frontal gyrus. These regions are consistent with prior studies showing that the frontal lobes are critical for controlled, intentional memory processes and are active during the attempt to retrieve relational information (e.g., Badgaiyan, Schacter & Alpert, 2002; Giovanello et al., 2004; Velanova et al., 2003; For a review, see Cabeza, 2006). Activity was also observed in several parietal regions, including left precuneus and right inferior parietal lobule. The parietal lobe has been implicated in mediating an attentional component of successful episodic memory (Daselaar et al., 2009; Cabeza et al., 2008). Critically, right anterior hippocampus was also active during successful retrieval of associations.

Of note, the MNI coordinates for the hippocampal activations in both conceptual (30, -20, -8) and perceptual (-38, -4, -18) associative priming, as well as in successful explicit retrieval (28, 0, -26), reveal involvement specifically in *anterior* hippocampus. Such engagement of anterior hippocampus is consistent with recent findings in the explicit memory literature (e.g. Giovanello, Schnyer, & Verfaellie, 2009), which have shown that different regions along the long axis make distinct contributions to relational processing. While posterior hippocampus has been shown to be involved in the structured reinstatement of perceptual information, anterior hippocampus has been shown to be involved in flexible retrieval operations (Giovanello et al., 2009). These findings, coupled with the present ones,

suggest a role for anterior hippocampus in relational processing, regardless of whether retrieval occurs at explicit or implicit levels.

Importantly, despite converging on the involvement of the hippocampus, there were two critical differences between implicit and explicit associative memory retrieval. First: these two forms of memory differed in their overall network of activations and, specifically, in the direction of activity. That explicit retrieval was associated with increases in neural activity, whereas implicit was primarily associated with decreases is consistent with typical differences between explicit and implicit memory (Schacter & Buckner, 1998a; Schacter et al., 2007). Second: the difference observed in the present study between item and associative priming does not mirror typical differences between item and associative recognition. More specifically, a functional division within the MTL has been demonstrated in the explicit memory literature, in which the hippocampus has been shown to make a relatively larger contribution to relational retrieval, while the surrounding parahippocampal cortex has been shown to make a relatively larger contribution to retrieval of single items (Davachi et al., 2003; but cf. Stark & Squire, 2003). Importantly, implicit retrieval does not appear to operate according to this dissociation. Despite diverging on the direction of activity in MTL regions, both measures of implicit relational retrieval (i.e., recombined>intact and re-colored>intact contrasts) involved the hippocampus as well as the entorhinal, perirhinal, and parahippocampal cortices. This finding is consistent with other fMRI studies of associative priming, which have also shown contributions from the hippocampus, parahippocampal cortex and perirhinal and entorhinal cortices to the implicit retrieval of associative information (Degonda, Mondadori, Bosshardt, Schmidt, Boesiger, Nitsch, Hock & Henke, 2005; Henke, et al., 2003; Schendan, Searl, Melrose & Stern, 2003). However, these studies



did not provide a direct contrast with item priming. In our study, implicit retrieval of item information (new>recombined trials) did not involve any MTL regions, even at a lenient threshold of  $p < .05$ . This dissociation between implicit associative and implicit item memory is fundamentally different from the dissociation between explicit associative and explicit item memory. Thus, the present study demonstrates an important difference between the neural bases of explicit and implicit memory, and establishes the first direct evidence that the hippocampus/PHG - relational/item dissociation that has been documented during explicit retrieval does not occur during implicit retrieval. Indeed, it would be important in future studies to investigate this issue further with a fully crossed design comparing conceptual and perceptual, associative and item, and explicit and implicit memory variables.

#### *Older Adults*

Experiment 6 also examined the effects of age on conceptual (object-object) and perceptual (object-feature) associative priming, item priming, and associative recognition. These will be discussed in turn. Regarding associative priming, the question of primary interest was whether age-related dysfunction in MTL regions would emerge on a task that is independent from strategic, PFC-mediated explicit retrieval processes and on which no age difference was found behaviorally. Young and older adults showed similar activations in some MTL regions during conceptual associative priming, with greater activity during intact relative to recombined pairs in left hippocampus and right entorhinal cortex in both age groups. However, young adults engaged additional MTL regions, with greater activity during intact relative to recombined pairs in right hippocampus and left parahippocampal gyrus as well. A similar pattern of age differences was found during perceptual associative priming. In young adults, the data showed decreased activity during intact trials relative to re-

colored trials in left hippocampus, right entorhinal cortex and left perirhinal cortex. In older adults, repetition-related deactivations were not observed in hippocampus, but rather in left anterior entorhinal cortex and right perirhinal cortex. Of note, the conjunction analysis of common activity in both age groups during perceptual associative priming did yield significant activity in 3 coordinates of left hippocampus. This difference between the conjunction analysis and the older adults' within-subjects analysis likely reflects differences in the statistical threshold, as the threshold of each age group individually was set to  $p < .07$  to achieve the conjoint probability of  $p < .005$  for the conjunction analysis. Overall, the pattern of age effects observed during perceptual associative priming is similar to the one observed during conceptual associative priming, and indicates that aging may be associated with weaker hippocampal function in the context of preserved rhinal cortex function. Although the pattern of weakened hippocampus coupled increased reliance on rhinal cortex has been observed during explicit testing (e.g., Daselaar et al., 2006), the replication of this pattern during associative priming was somewhat surprising given age-equivalence on the behavioral measure. This interesting finding will be discussed in more detail in the General Discussion.

Unlike associative priming, during which I expected the involvement of MTL regions, MTL involvement was not anticipated during item priming. Consistent with this hypothesis, no MTL regions of activity were observed in young adults during item priming. The critical question for present purposes was whether aging would be associated with a similar or different network of non-MTL neural regions as young adults during item priming. Interestingly, there was a substantially wider network of repetition-related deactivations in young adults relative to older adults. As described earlier, young adults showed activity that was greater for new trials than recombined trials in several temporal, parietal, and frontal

regions, as well as anterior cingulate. The involvement of these regions is consistent with previous studies of speeded object classification (Buckner, et al., 1998; Koutstaal, et al., 2001) and the role of each of these regions during object priming was considered previously in the discussion of the young adult findings. Regarding the effects of aging: older adults showed item repetition-related deactivations in middle frontal gyrus (BA 11), consistent with increased ease of decision processes for the classification task. Older adults also showed deactivations in the superior frontal region of right precentral gyrus (BA 6) and the superior parietal region of left postcentral gyrus (BA 43), both of which have been implicated in motor processes (e.g., Agosta et al., 2009) and may reflect increased ease of motor response on the classification task. However, the wider distribution of repetition-related deactivations observed in young adults may indicate some loss of efficiency of processing in age during speeded object classification. For instance, deactivations were observed in several parietal regions in young adults that were greater than in older adults. It is uncertain precisely how these parietal deactivations contribute to priming in young adults. However, this age effect is consistent with recent data showing an age-related reduction in parietal deactivations during face-name associative encoding (Miller et al., 2008). More generally, the result of more widespread deactivation in young adults is consistent with some findings of under- or dedifferentiated- recruitment of task-related neural regions (e.g. Logan et al., 2002; Morcom et al., 2007).

Given that older adults showed under-recruitment in some task-related regions, an important question was whether they simultaneously showed over-recruitment in non-task-related neural regions. As described previously, several prior studies (Bergerbest et al., 2009; Cabeza, 2002; Morcom et al., 2003; Reuter-Lorenz & Stanczak, 2000; Stebbins et al., 2002)

have shown the right PFC to be a common region of over-activation in healthy older adults compared with young adults. As such, an important question was whether young and older adults would differ in the engagement of anterior cortical regions during both item and associative priming. A similar pattern emerged during conceptual associative priming, perceptual associative priming, and item priming, such that older adults but not younger adults showed increases in activity in frontal regions. Increases refer to activity that was greater during intact relative to recombined trials for conceptual associative priming, greater during intact relative to re-colored trials for perceptual associative priming, and greater during recombined relative to new trials for item priming. In contrast to the older adults, young adults did not show increases in activity for any of these contrasts. Instead, frontal regions were observed in younger adults only for the reverse contrasts that assessed *deactivations*. The specific regions within the frontal lobe that showed deactivations in young adults and activations in older adults are listed systematically in the results section as well as in Tables 11-18. Thus, despite differences in overall networks of activated regions during priming of object-object and object-feature associations, as well as priming of objects without an associative component, aging appears to be linked with additional recruitment of frontal regions that is not observed in young adults.

There are several possible reasons for these frontal activations. If activity in these regions were associated with successful aging, such that non-task-related frontal regions were recruited to compensate for dysfunction in task-related regions, one would expect the amount of frontal activity to correlate with performance on the behavioral task. Importantly, the only specific frontal region commonly activated by older adults across conceptual and perceptual associative priming as well as item priming was right DLPFC in BA 9. For this reason, task-

activity correlational analyses focused on this region. The results of these analyses were largely consistent with predictions of the compensatory account. In particular, significant negative correlation was observed in older adults between activity in BA 9 during intact trials and intact reaction times. No relationship was found between activity in this region and intact RTs in young adults. Likewise, a negative correlation approached significance in older adults between right DLPFC activity during recombined trials and recombined RTs that. No relationship was found between activity in this region and recombined RTs in young adults. Lastly, there was a negative correlation RTs that approached significance in older adults between right DLPFC activity during re-colored trials and re-colored, whereas no relationship was found between activity in this region and re-colored RTs in young adults. Of note, if activity in right BA 9 were a reflection of a generalized ability to perform the reaction time task, then a relationship would be expected between neural activity in right BA 9 and RTs during new trials. However, no relationship was found, indicating that the recruitment of right DLPFC is not generalized to the task but is rather specific to the priming effects. Additionally, if right DLPFC activity reflected the adoption of additional cognitive processes to aid in performing the task, such as monitoring, activity would again be expected to be associated with reaction time during new trials. As such, the non-relationship between new trial RTs and BA 9 activity argues against this possibility. Lastly, the fact that activity in right BA 9 during intact trials positively correlated with activity in right hippocampus fits with the interpretation of DLPFC activation as an indication of successful aging (e.g., Cabeza et al., 2002). However, is worth noting that no significant correlations were observed between reaction times and activity in any frontal regions other than in right BA 9. For this

reason, it is possible that the different subregions within the frontal lobe may be recruited for different purposes.

A final point in regards to interpreting the age differences in recruitment of frontal regions during priming: it should be highlighted that results from the voxelwise analyses yield *relative* contrasts. That is, the between-subjects analysis of intact greater-than recombined activity that is greater in older than younger adults will, by definition, yield the same regions as the analysis of recombined greater-than intact activity that is greater in younger than older adults. As such, it is impossible to know based only on the voxelwise analysis whether the frontal regions observed in these contrasts were driven by *increased* activity in older adults or in fact *decreased* activity in young adults. For this reason, beta values were extracted from the ROI analysis to identify the direction of activation differences. The parameter estimates for intact and recombined trials are graphed in Figure 1 and for intact and re-colored trials are graphed in Figure 3. Interestingly, these parameter estimates show that the significant difference in activity is driven by *both* decreased activity in young adults coupled with increased activity in older adults. More specifically, relative to baseline in the regression model for the implicit test run, the right DLPFC in BA 9 was deactivated during both intact and recombined trials in young adults, with intact trials more deactivated than recombined. Fully reversing this pattern, relative to baseline in the regression model for the implicit test run, right DLPFC in BA 9 was activated during both intact and recombined trials in older adults, with intact trials more active than recombined trials. The identical pattern occurred for the intact versus re-colored contrast, with intact trials more deactivated than re-colored trials in young adults (and both deactivated relative to baseline), but intact trials more active than re-colored trials in older adults (and both active

relative to baseline). These cross-over interactions thus support the classification of right BA 9 activation in older adults during priming as over-activations, rather than simply weaker deactivations.

Thus, Experiment 6 documents the first evidence linking increased activity in right dorsolateral PFC with successful priming of new associations in older adults. The results show that associative priming joins other manipulations in the literature that are associated with a re-organization of the neural regions associated with cognitive tasks in healthy aging, in particular the recruitment of prefrontal cortical regions that correlates with better cognitive performance. The one example in the literature that has reported a reversed direction of prefrontal recruitment is by Bergerbest et al. (2009), who observed additional age-related *deactivations* in right PFC (BAs 8, 9, and 46) during conceptual (item) priming. One possible explanation for this difference in the direction of age-related recruitment of the PFC is that Bergerbest et al. (2009) only reported activity that was greater for new than repeated stimuli. That is, had they examined (or reported) activity that was greater for repeated than new stimuli, it is possible that activity in additional frontal regions would have been observed.

Lastly, in addition to associative and item priming, Experiment 6 also examined the effect of age on associative recognition. Based on prior studies of explicit item (Giovanello et al., 2004; Gutchess et al., 2005; Grady et al., 2005) and relational (Giovanello et al., 2009) retrieval tasks that engaged both MTL and PFC regions in young adults, I predicted that age-related explicit associative recognition deficits would be associated with MTL dysfunction coupled with increased engagement of frontal regions. In the present experiment, successful explicit associative retrieval was linked with a widely different network of activated regions

in young and older adults, with only left cingulate gyrus commonly activated. Importantly, young but not older adults showed significant activity in the hippocampus. In regards to whether recruitment of prefrontal regions accompanied this age-related MTL dysfunction during successful associative recognition, the pattern is less clear than during associative priming. Left middle frontal gyrus (BA 10) and left inferior frontal gyrus (BA 45) were more active in older than younger adults, however bilateral inferior frontal gyrus (BA 47) and right middle frontal gyrus (BA 11) were more active in young than older adults. Thus, unlike associative priming, during which younger adults did not elicit activity in any frontal regions that was greater than older adults, the role of the frontal lobes during successful associative recognition appears to be divided. Furthermore, the correlational analyses showed no relationship between hits (or correct rejections) and activity in either of the frontal regions more activated in older adults (left BA 10 and left BA 45) during each respective recognition event. As such, the present results do not necessarily speak to the function of the age-related differences in frontal lobe activation during successful associative recognition. An important question that may be related to this uncertainty is whether the differences in activated regions during associative recognition reflect true age differences rather than differences in task performance. Young adults performed significantly better than older adults on the behavioral accuracy measure; thus, it is possible that the differences in activated neural regions were a function of task performance rather than an effect of age. To examine this possibility, proportions of correct rejections to recombined pairs in young adults were correlated with activity in left BA 10 and in left BA 45 during correct rejection trials (i.e., the two frontal regions that were more active in older than younger adults) to determine whether young adult subjects who performed worse on the task would yield more activity in either of these



regions. Neither of correlation was significant ( $ps > .1$ ). However, the raw number of correct rejection trials per subject were relatively small (ranging from 8 to 17 modeled correct rejection events per subject), coupled with only 14 subjects in the analysis; it is possible that with greater power to detect reliable differences, the correlations could reach significance and contribute to the question of task performance effects. A potentially informative way to examine this question in the future would be to compare differences in brain activity among divided high- and low-performing young adult groups within a larger overall sample.

## CHAPTER XVII

### GENERAL DISCUSSION

To review the overarching goals and theoretical motivation of the present series of experiments: Studying implicit memory for new associations is an important way to examine the scope and limits of impaired and preserved memory function in healthy aging. A well-established finding in cognitive aging research is a larger age-related decline in memory for contextually-rich episodic events, relative to memory for single items. Importantly, strategic memory retrieval processes and associative/binding processes are known to work together intricately to support episodic memory, at both cognitive and neural levels. As of yet, however, it is uncertain whether age-related declines in episodic memory stem from impairments in one or both of these processes. Indeed, the hypotheses of impaired strategic conscious recollection and impaired binding processes share several common predictions, and both are consistent with the typical finding of disproportionately impaired explicit memory for associative information (i.e., items in their studied context) relative to memory for item information in the absence of contextual detail (Bayen et al., 2003; Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995). Of note, however, these hypotheses offer different predictions about the status of implicit memory. If episodic memory declines stem from an age-related impairment in binding processes, emphasizing deficient associative encoding, then an age-related impairment in implicit associative memory is predicted. If episodic memory declines stem from an age-related impairment in

strategic recollection, emphasizing deficient conscious associative retrieval, then no age difference in implicit associative memory is predicted.

To date, mixed findings have emerged from studies of implicit associative memory in aging, with perceptual associative implicit memory appearing to be preserved (Gibson, Brooks, Friedman & Yesavage, 1993; Light, LaVoie, Valencia-Laver Albertson-Owens & Mead, 1992; Lloyd-Jones, 2005; Wiggs & Martin, 1994) and conceptual associative implicit memory appearing to be impaired (Ergis, Van der Linden, & Deweer, 1998; Howard, Fry, & Brune, 1991; Howard, Heisey & Shaw, 1986; Monti et al., 1997; O'Hanlon, Wilcox & Kemper, 2001; Spieler & Balota, 1996). However, some commonly used conceptual associative priming tasks been difficult to dissociate from explicit retrieval processes (Graf & Schacter, 1985; Kinoshita, 1999; O'Hanlon et al., 2001; Reingold & Goshen-Gottstein, 1996; Shimamura & Squire, 1989; Wegesin et al., 2004); thus, their status in aging has been uncertain.

In 6 experiments I presented a novel paradigm of conceptual associative priming. Using an associative version of a speeded size classification task, Experiment 1 showed no age difference in associative priming. Because the task-specific classification in Experiment 1 may have involved not only semantic information about object size but also a perceptual/spatial judgment, Experiment 2 tested whether the results of Experiment 1 would generalize to a task using a different semantic category. Using a speeded inside/outside classification task, Experiment 2 again found no age difference in associative priming. The perceptual manipulation (recombination of object colors) had no affect on priming, supporting the classification of priming as conceptually-driven. Experiment 2 also replicated the typical age-related impairment in associative recognition that followed the same

incidental encoding manipulation. This pattern shows that the pattern of findings on the implicit measure could not be explained only by age-equivalence in incidental encoding, but rather as a combined effect of incidental encoding and implicit retrieval. Next, demonstrating that intentional encoding and retrieval in fact eliminates associative priming via a slowing of reaction times to intact trials, Experiment 3 showed that associative priming in the inside/outside speeded classification task cannot be explained by explicit contamination. In Experiment 4, decision cue inversion reduced priming in both age groups during speeded classification of single objects. In Experiment 5, cue inversion eliminated priming on the associative version of this task. These two experiments thus showed that both older and younger adults form an incidental episodic association between the stimuli and the task-specific response. Taken together, the behavioral experiments provide an important example of a form of associative processing that is unimpaired in older adults, at both encoding and retrieval stages. Below, I consider the results of each of the behavioral experiments in more detail, followed by further analysis of the fMRI study.

As described, Experiments 1, 2 and the same-cue condition in Experiment 5 (as well as the behavioral data from Experiment 6), showed that older adults can show implicit memory for new meaningful associations to the same extent as young adults. Of note, insufficient power to detect reliable age differences is not a viable explanation for the results, as the raw RT scores were actually in the direction of greater differences in old than young. The lack of age differences contrasts with some previous studies (e.g., Ergis et al., 1998; O'Hanlon et al., 2001), in which young but not older adults demonstrated priming of new associations. Although the effects in prior studies were interpreted as an age-related impairment in the formation of new conceptual associations, the paradigms employed have

been difficult to dissociate from explicit memory in the young adult literature (Bowers & Schacter, 1990; Kinoshita, 1999). The present experiments used a speeded associative classification paradigm to test age differences. This reaction time paradigm was selected based on findings in the literature showing that explicit contamination is less likely to occur on reaction time tests relative to accuracy tests of implicit memory (Horton, et al., 2001; Light et al., 2000; Richard-Klavehn & Gardiner, 1998). The pattern of equivalent associative priming in Experiments 1 and 2 suggests that the reason prior conceptual associative priming paradigms found age differences is not simply because older adults are impaired in the process of creating new meaningful associative links. Rather, the previous findings of age-related impairment in conceptual associative priming might instead be explained by the potentially confounding involvement of elaborative encoding and strategic retrieval processes that are independently affected by aging.

Of note, three specific current findings argue against the possibility – or utility – of explicit contamination during the present speeded classification paradigm. First: Experiment 2 demonstrated an age-related dissociation between implicit and explicit associative memory. While no age difference was found for implicit associative memory, a substantial age effect emerged for explicit associative memory. If explicit retrieval processes were to be used to aid performance on the implicit test, the age-related dissociation between explicit and implicit memory suggests that the young adults would have benefitted more than the older adults. The second form of evidence against explicit contamination comes from the analysis of subjects divided based on reported use of an explicit retrieval strategy. As shown in Tables 3 and 4, young and older subjects who claimed on the awareness questionnaire to have used explicit retrieval produced a similar pattern of reaction times in each of the retrieval

conditions. The third form of evidence against the involvement of explicit processes in the paradigm employed comes from Experiment 3, in which associative priming was eliminated via a manipulation of incidental versus intentional encoding, despite the reverse effect on associative recognition. Future use of the associative speeded classification paradigm would benefit from a thorough analysis of whether, and how, it responds to additional encoding manipulations known to affect explicit memory, including levels of processing or divided attention. It is curious that associative priming was eliminated in Experiment 3 despite no difference in priming based on reported explicit strategy use in Experiments 1 and 2. One possible explanation for this difference is that explicit associative recognition performance following incidental encoding may not have been high enough to support utility of an explicit retrieval strategy. In contrast, when explicit memory for studied trials was improved via a manipulation of intentional encoding, performance for studied trials (i.e., even during implicit testing) may have then become affected by strategy use. This possibility is consistent with the finding that the elimination of priming was driven specifically by a slowing of reaction time to intact pairs, the only stimuli that were associated with a prior associative response. This slowing effect on the intact trials (i.e., studied trials) is consistent with other studies in the literature (e.g., Horton et al., 2001) showing that explicit strategy requires more time than automatic retrieval. Given this possibility, it would be especially important in future studies to conduct Experiment 3 in an older adult sample. If intentional encoding were to improve young adults' explicit memory to a significantly larger extent than older adults, it would be of considerable theoretical interest to determine whether the reverse effect on associative priming would occur in a similarly graded manner between the age groups.

Future research will be needed to delineate the cognitive mechanism driving the

dissociative effect of incidental and intentional encoding on implicit and explicit associative memory in Experiment 3. One feature of Experiment 3 that could have contributed to the dissociation is that performance on the explicit recognition test may have benefitted from practice effects more than the implicit reaction time task. Intentional encoding always followed incidental encoding; that is, the order of encoding manipulations could not be counterbalanced, because completing the intentional encoding task first would very likely influence strategies during the subsequent encoding session, even if subjects were instructed otherwise. Importantly, the transfer between the two implicit tests in terms of overall cognitive operations may not have been as high as the transfer between the explicit tests. For instance, although the instructions were the same in both implicit tests, it is possible that the intentional encoding manipulation induced the adoption of an explicit strategy on the second implicit test. In this case, the overall cognitive approach to the two implicit tests would be lower than the approach to the explicit tests, in which strategy would have been a component in both. In turn, practice effects may have been minimized or prevented in the implicit test, where as explicit recognition performance may have benefitted from general task-related improvement. In summary, although further data are needed to clarify the mechanism of why intentional encoding eliminates associative priming, the critical point for present purposes is that it offers a strong argument against explicit contamination in the speeded associative classification task.

While the study of associative priming offers one way in which to examine the effect of aging on nonconscious (i.e., unintentional) associative processing, the study of rapid response learning offers a complementary method. As described earlier, studies examining the rapid learning of the association between a stimulus and a task-specific response required

for that stimulus have recently provided key evidence for a mechanism underlying repetition priming on speeded classification tasks (Dobbins et al., 2004; Horner & Henson, 2008; Horner & Henson, 2009; Schnyer et al., 2006; Schnyer et al., 2007). Although previous theoretical accounts, such as a neural sharpening mechanism (Wiggs & Martin, 1998), have been successful in explaining certain instances of priming, especially tasks in which the stimulus is changed from study to test (Schacter, Wig & Stevens, 2007), rapid response learning may be more successful in accounting for priming on speeded classification tasks in which the stimulus remains constant (Dobbins et al., 2004; Horner & Henson, 2008, 2009; Schnyer et al., 2007; see also Logan, 1988). Experiments 4 and 5 provide further evidence of the hypothesis that rapid response learning underlies priming on speeded classification tasks. Experiment 4 showed that cue inversion reduced priming using a speeded inside/outside judgment, and in Experiment 5 cue inversion eliminated priming on an associative version of this task. Importantly, both young and older adults demonstrated rapid response learning. Thus, older adults formed an incidental stimulus-response association to the same extent as young adults.

Of note, Dobbins et al. (2004) found evidence of neural priming in left PFC when the classification decision cue was the same from study to test, but cue inversion disrupted priming in this region; this pattern provided key evidence that rapid response learning reflects increased automatized processing in the context of decreased executive processes. A population with an impairment in strategic retrieval processes should thus benefit by relying on prior responses, and the lack of age differences in rapid response learning fits with this hypothesis. A functional neuroimaging approach would be an important future direction for Experiments 4 and 5, to determine whether, under conditions of cue reversal, changes in



neural priming occur similarly in both age groups.

Experiment 5 also produced a dissociation between item priming and associative priming, such that cue reversal eliminated associative priming (in which a repeated pair was compared with a recombined pair) but had no effect on item priming (in which a recombined pair was compared with a new pair). This dissociation is particularly interesting given that the item-level decision did not change from study to test. That is, the decision for any individual item remained constant from study to test, regardless of whether that item appeared in an intact pair or a recombined pair. For instance, the classification decision for the item *oven*, when paired initially with *tree*, would be that it is more likely to be found inside a house. The decision cue for *oven* then remained constant, regardless of whether its associative pairing was intact at test (*oven–tree*) or was recombined (*oven–basketball*). Because the prior object-level response always remained appropriate, one might have reasonably assumed that this preserved correspondence would contribute to facilitation of performance in both item and associative priming. However, the preserved priming of recombined pairs relative to novel pairs was unaffected by whether or not the prior response remained appropriate (i.e., was independent of whether the previously selected or previously not selected probe was the correct response). One possible explanation for this finding relates to the high degree of perceptual specificity that appears to accompany rapid response learning. For instance, Schnyer et al. (2007) found that cue reversal did not reduce priming on speeded size classification for trials in which a different exemplar of a studied object had been presented. In the present study, the comparison of recombined versus new pairs offers a measure of item priming, but the stimulus as a whole was not visually perceived at study. Although the manipulation by Schnyer et al. (2007) and the present study are very different

paradigms, they may converge on the suggestion of a high degree of perceptual specificity in the effect of rapid response learning on speeded classification tests. In turn, the dissociation between item and associative priming in Experiment 5 indicates that rapid response learning does not underlie all forms of priming, even within speeded classification tests, but rather occurs for tasks or environments in which the stimulus remains constant (Logan, 1988; Schacter et al., 2004; Schnyer et al., 2007).

To summarize the behavioral studies, no evidence was provided of an age difference in speeded associative size or inside/outside classification of objects, nor in rapid response learning within repetition priming or associative priming. Taken together, the present studies thus provide an important example of a form of associative processing that is unimpaired in older adults. These results can be used to inform the broader theoretical frameworks of episodic memory decline. The hypotheses of impaired strategic recollection versus impaired binding processes share several features, such that some aspects of the current data do not necessarily distinguish between these theories. For instance, the age difference in associative recognition in Experiment 2 coupled with no age difference in item recognition is consistent with a large set of findings in the literature showing a substantially larger age effect in memory for associative/contextual details relative to single content items (Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995). While this general pattern has been interpreted as an age-related deficit in associative processing (Chalfonte & Johnson, 1996; Naveh-Benjamin, 2000), this pattern is also consistent with impaired recollection coupled with preserved familiarity (Jacoby, 1999; Jennings & Jacoby, 1999; Naveh-Benjamin et al., 2009). More specifically, as in many previous studies (e.g., Naveh-Benjamin, 2000; Naveh-Benjamin et al., 2009), the lower associative recognition accuracy in older adults in each of the current

studies was driven by an increased rate of false alarms to recombined pairs. The recombined pairs thus acted as lures, supporting the hypothesis that older adults do recognize the individual units but not the way in which units are bound together. This pattern of an increased false alarm rate to recombined pairs has been used as evidence that older adults are less able to use recollection of specific contextual episodes to counteract the influence of item familiarity (Jacoby, 1999).

Although the recognition data in Experiment 2 are supportive of both a binding deficit and a recollection deficit, the fact that a larger age difference in associative relative to item memory was only observed on the explicit measure is consistent with an hypothesis that emphasizes impairments in recollection. More specifically: at the retrieval stage, the results of Experiment 2 are supportive of a specific age-related decline in intentional/strategic retrieval of associations, rather than a generalized decline in associative processing or even a generalized decline in strategic, consciously-controlled memory processes (which would also affect item recognition). At the encoding stage, the current results are supportive of age-related preservations in associative encoding, at least under incidental conditions. Although there has been some evidence of an age-related (explicit) memory impairment when preceded by incidental associative encoding, albeit smaller than under intentional conditions (Old & Naveh-Benjamin, 2008), the results in the present experiments fit with a growing body of research showing that when associative tasks do not require elaborative encoding or strategic retrieval mechanisms, older adults perform at the level of young adults (et al., 2006; Howard, Howard, Dennis, LaVine & Valentino, 2008; Howard, Howard, Dennis, Yankovich & Vaidya, 2004). Interestingly, not all the literature is suggestive of an age-related deficit in intentional associative encoding, either. For instance, while older adults typically show

poorer recall performance, they actually chunk information similarly when to-be-learned sequences are not longer than 6 items (e.g., Allen & Coyne, 1988, Allen & Coyne, 1989; Allen & Crozier, 1991). When sequences are longer, older adults do show deficits in chunking (Naveh-Benjamin, Cowan, Kilb, & Chen, 2007), an effect that may be driven by age-related limitations in generalized processing resources.

Although the finding of unimpaired implicit associative memory can be seen as evidence that the items were initially encoded together with their presented context, an alternative possibility worth considering is that implicit and explicit memory are sensitive to different features of an encoded event. That is, it may be the case that implicit and explicit memory do not share access to the same mnemonic information, implying that the aspects of an encoded event that are available for implicit memory are fundamentally different from the aspects that are available for explicit memory. This would suggest that only certain features of the initial stimuli may have been encoded and bound by the older adults. Research in the neuropsychological literature distinguishes between systems that support declarative (explicit) memories, which are described as fundamentally flexible in nature, and nondeclarative (implicit) memories, which are fixed and rigid (Cohen, Poldrack & Eichenbaum, 1997). The characteristics of flexible versus fixed memory representations can be seen as an analogue to the distinction between relational and conjunctive binding that was described in the discussion of Experiment 6. Little is currently known about the flexibility of implicit associative memories. It would be important in a future study to examine the effects of aging on flexible versus fused associative memory representations, in order to help determine whether equivalent priming in young and older adults reflects access to the same or a different memory representation.

In addition to the current behavioral studies, the present dissertation involved a functional neuroimaging study that examined the neural basis of associative memory. Specifically, Experiment 6 was a replication of Experiment 2 using event-related fMRI, to determine the roles of MTL and PFC regions during associative priming and associative recognition in young and older adults. More generally, a functional neuroimaging approach complements the behavioral findings in trying to understand the neural basis of why the present series of experiments observed no age difference in implicit memory for new associations, given the well-established findings of large age differences in explicit memory.

Experiment 6 contributes to a growing literature that highlights the importance of MTL regions during multiple types of relational processing. Indeed, active hippocampus was observed in both young and older adults during both implicit and explicit retrieval of new object-object associations. In addition, while the primary focus of each of the current experiments was priming of new conceptual associations, Experiment 6 also made use of the re-colored trials to examine a form of perceptual (i.e., object-color) associative priming. As described previously, deactivations in MTL regions were observed during priming of these object-feature associations. The involvement of MTL regions is consistent with literature showing that the medial temporal lobes contribute to the initial binding of intra-item (i.e., item- feature) relationships at encoding (Cansino, Maquet, Dolan & Rugg, 2002; Prince, Daselaar & Cabeza, 2005), even under rapid, incidental conditions (for a review, see O'Reilly & Rudy, 2001). Of note, however, the neuroimaging literature has not always observed MTL activity during priming when the stimuli involve alterations to intra-item contextual details (e.g., changes in perceptual modality, Buckner et al., 2000, Carlesimo et al., 2003). Indeed, the current literature appears to lack a systematic operationalization of

when implicit intra-item retrieval reflects a type of associative priming, rather than a type of item priming. Although the involvement of MTL regions during intra-item priming could be seen as consistent with *associative* status, whereas priming that does not involve MTL regions is consistent with *item* status, this method of classification is susceptible to circular reasoning. Establishing a classification system for what comprises an association versus an item is a critical direction for future research, at both a behavioral and neural level.

The finding of active MTL during unintentional relational retrieval mirrors the role of this region during incidental relational encoding. For instance, Jackson and Schacter (2004) found that the initial encoding of word pair trials that were later remembered successfully was correlated with activity in left anterior hippocampus and bilateral entorhinal cortex, supporting the critical role of these regions in successful binding under incidental conditions (see also Hannula & Ranganath, 2008 and Hannula & Ranganath, 2009 for similar findings). Likewise, Schendan et al. (2003) examined a sequence learning (serial reaction time) task, a form of spatiotemporal associative learning that produces faster response times to a cue for repeated sequences relative to randomly generated new sequences. After the serial reaction time task, subjects completed one of several explicit tests of the preceding sequences. Both implicit and explicit retrieval correlated with bilateral MTL activity (including hippocampus, entorhinal cortex and parahippocampal cortex), although MTL activity correlated with PFC activity only during the explicit test. Moreover, participants who were classified as unaware of the repeating patterns showed MTL activation that was indistinguishable from those classified as test-aware, and the MTL activity during implicit learning was uncorrelated with the successful performance on the explicit sequence tests, providing evidence that learning was nonconscious. These findings are consistent with the data from Experiment 6 in

highlighting the importance of MTL regions in associative-binding processes independently from level of awareness.

Relatedly, while the importance of examining explicit contamination during associative priming was discussed previously in terms of the behavioral findings, this issue is independently relevant for the neuroimaging data. fMRI of priming studies must also consider the possibility that brain activity is affected by awareness of the study-test connection and the potentially ensuing adoption of an explicit retrieval strategy. As described previously, Experiment 3 demonstrated that explicit retrieval processes could not explain the behavioral priming effect between intact and recombined trials, as the same manipulation that induced improved explicit performance eliminated associative priming. This dissociation helps to explain why the present fMRI study produced a different result from some prior tasks of associative priming that observed activity in prefrontal cortex and which may have involved concurrent explicit processes (e.g., Bayadgian, et al., 2003). Regarding this general concern of unintentional explicit involvement, however, a potential limitation of Experiment 6 is that during explicit testing, subjects did produce more correct responses to intact pairs (hits) than to recombined pairs (correct rejections). This raw memory difference for the two types of trials during explicit testing leaves open the possibility that conscious awareness of the study-test connection during implicit testing would have been more likely for intact trials than for recombined. If this were the case, then one could presumably argue that neural activations more associated with intact trials than recombined could be confounded by explicit processes. However, this possibility is unlikely in the present study. Explicit retrieval is not only dependent on the hippocampus but on connectivity between the hippocampus and prefrontal and parietal regions, with intentional retrieval and successful

recollection associated with increased activity in *both* hippocampus and PFC (Schacter & Buckner, 1998b) as well as parietal regions (Cabeza et al., 2006; Wilding, 2000). The current study replicated this typical pattern in during explicit retrieval, yet during implicit retrieval there were *increases* in activity in hippocampus coupled with *decreases* in activity in prefrontal and parietal regions. The negative relationship observed between these regions during conceptual associative priming argues against the possibility that the activity in the hippocampus was driven by explicit processes. Instead, it is more supportive of the notion that relational binding is the common mechanism on which both explicit and implicit associative retrieval rely.

In addition to examining the role of the hippocampus and adjacent MTL regions during implicit associative retrieval in young adults, Experiment 6 also examined the effect of aging on the neural basis of associative priming. The findings for each specific contrast were considered in detail in the discussion section for Experiment 6. More broadly, however, an important question is whether the neural activation findings can contribute to the general theoretical frameworks of associative-binding versus strategic recollection deficits. As described earlier, although some aspects of the present behavioral studies are equally supportive of a binding deficit and a recollection deficit, the implicit testing data are more supportive of a deficit in recollection. The neuroimaging results of implicit tests are somewhat less straightforward. For instance, preserved neural priming could be seen as indicative of preserved encoding operations. Indeed, deactivations associated with repeated but not new stimuli are an indication of having initially successfully perceived or processed these stimuli. Thus, a similar pattern of deactivations between young and older adults observed in both item and associative priming supports an emphasis on deficient explicit



associative retrieval, rather than encoding. However, the neural regions of deactivations were not identical between young and older adults. Thus, one possibility is that priming in older and younger adults – though of equal magnitude – may reflect the encoding or retrieval of different memory representations. Alternatively, it may be the case that older adults use some different neural regions to access the same memory representation. Future research should work toward distinguishing between these possibilities.

An additional way to assess the distinction between an associative-binding deficit and a recollection deficit is to consider the age differences in activation in the hippocampus versus the rhinal cortex. During conceptual associative priming, young and older adults showed similar activations in some MTL regions, with greater activity during intact relative to recombined pairs in left hippocampus and right entorhinal cortex in both age groups. However, young adults engaged additional MTL regions, with greater activity during intact relative to recombined pairs also in right hippocampus and left parahippocampal gyrus. A similar pattern of age differences was found during perceptual associative priming. In young adults, the data showed decreased activity during intact trials relative to re-colored trials in left hippocampus, right entorhinal cortex and left perirhinal cortex. In older adults, repetition-related deactivations were not observed in hippocampus, but rather in left anterior entorhinal cortex and right perirhinal cortex. Overall, the pattern of age effects observed during perceptual associative priming is similar to the one observed during conceptual associative priming, and indicates that aging may be associated with weaker hippocampal function in the context of preserved function in rhinal cortex. This pattern is consistent with other recent findings (e.g., Daselaar et al., 2006) indicating that different subregions within the MTL may be differentially affected by aging, with weaker activity in hippocampus but preservations or

even over-recruitment of rhinal cortex. In the explicit memory literature, reduced activity in hippocampus in the context of increased activity in rhinal cortex has been interpreted as consistent with an impairment in recollection coupled with increased reliance on familiarity (Daselaar et al., 2006). Indeed, there is a large body of research showing a greater contribution of the hippocampus to recollection, while the rhinal cortex contributes more to familiarity (for a review, see Brown & Aggleton, 2001; Yonelinas, Ranganath, and Eichenbaum, 2008).

However, it is uncertain what accounts for the difference between these regions during implicit associative memory. One possibility is that the rhinal cortex activity observed typically during familiarity and in the present study during associative priming may reflect a common mechanism of conceptual or perceptual fluency. Familiarity is particularly sensitive to conceptual processing (Wagner & Gabrieli, 1998), and the reengagement of features that gives rise to priming may simultaneously influence or bias judgments of familiarity (Rajaram & Geraci, 2000). Moreover, a few studies have recently identified an involvement of the perirhinal cortex during perceptual discrimination of objects and faces (Barense, Henson, Lee & Graham, 2009) as well as during conceptual priming (O’Kane et al., 2005; Voss, Hauner & Paller, 2009). As such, it is possible that during associative priming, young adults rely more on the reengagement of binding processes (linked with the hippocampus), while older adults may rely more on more a generalized mechanism of perceptual or conceptual fluency (linked with the rhinal cortex). Further data are needed to clarify the precise contribution of the rhinal cortex to processes involved in long-term memory, both explicit and implicit. More generally, however, the present study may represent a case in which young and older adults engage in different component processes to yield a similar behavioral result.

In addition, older adults elicited activity in frontal regions not observed in young adults that correlated with priming. This study documents the first evidence that additional frontal recruitments operate during associative priming, on a task in which no age differences are found behaviorally. During explicit associative retrieval, older adults showed reduced MTL function in the context of increased PFC activity. Taken together, the results suggest that the relative contribution of MTL versus PFC regions to associative memory declines in older adults is moderated by the nature of the task. However, an absence of age differences in the behavioral measure does not necessarily map onto the same pattern of neural activations in the two age groups. This finding is consistent with patterns of structure-function reorganization in aging (e.g., Cabeza, 2002; Cabeza et al., 2002; Reuter-Lorenz & Stanczak, 2000). Experiment 6 documents the first evidence linking increased activity in right dorsolateral PFC with successful priming of new associations in older adults. The results show that associative priming joins other manipulations in the literature that are associated with a re-organization of the neural regions associated with cognitive tasks in healthy aging, in particular the recruitment of prefrontal cortical regions that correlates with better cognitive performance.

In conclusion, the current data contribute several novel findings to the memory, aging, and cognitive neuroscience literatures. Collectively, the findings provide evidence of a form of associative processing that is preserved in healthy aging. These findings are of considerable theoretical interest, given the tendency to observe relative decline in older adults across a range of associative tasks. Within the broader context of priming, the current data show that conceptual associative priming joins other manipulations in the literature that show no or minimal age difference for implicit memory tasks that use reaction time rather

than accuracy as the dependent measure (Light et al., 2000), and that require identification/classification rather than production-based responses (Fleischman & Gabrieli, 1998). Within the broader context of age-related episodic memory decline, these experiments suggest that older adults can encode new meaningful associations and access them using automatic retrieval processes, but have difficulty with the conscious, strategic retrieval of the same information. In its broadest context, understanding the nature and source of age-related impairments and preservations in memory processes is not only of theoretical importance, but also has ecologically-valid implications for older adults' day-to-day memory function; the ability to bind elements together into a rich, contextual representation is what allows for successful and coherent memories of everyday events. Moreover, the convergence of behavioral and cognitive neuroscientific approaches can help to distinguish between cognitive and cerebral changes that accompany healthy aging from those of pathological aging. The combination of multiple approaches will help to contribute to a more comprehensive picture of cognitive aging.

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Table 1  
*Mean scores on battery of neuropsychological tests*

	MMSE	ANART	Vocab	Trail Making A	Trail Making A Errors	Trail Making B	Trail Making B errors	Morn/Eve
	Experiment 1*							
OA	29.30	42.87	56.48	27.65	0.00	63.83	0.00	58.59
	Experiment 2**							
YA	29.97	39.62	49.32	20.61	0.00	49.78	0.00	41.03
OA	29.13	43.58	60.25	33.08	0.00	65.58	0.08	60.46
	Experiment 4***							
YA	30.00	40.21	55.78	22.45	0.00	58.13	0.00	38.65
OA	29.78	46.28	59.29	30.78	0.00	69.11	0.00	60.17
	Experiment 5****							
YA	29.83	31.23	47.32	18.64	0.04	55.94	0.00	52.78
OA	29.09	41.26	55.96	34.87	0.00	74.74	0.00	60.52
	Experiment 6							
YA	30.00	35.78	51.45	18.75	0.00	48.13	0.00	50.13
OA	29.40	45.60	61.73	31.80	0.04	65.80	0.21	60.27

\* *YA scores in Exp. 1 were not collected*

\*\* *Includes data from 31/32 OAs*

\*\*\* *Includes data from 18/24 OAs*

\*\*\*\* *Includes data from 31/32 OAs*

Table 2

*Mean reaction time (and standard deviation) in msec for each for each implicit trial type in Experiments 1 and 2*

	Intact	Re-colored	Recombined	New
Experiment 1				
Young	969 (183)	N/A	1039 (179)	1101 (198)
Old	1320 (322)	N/A	1431 (272)	1531 (368)
Experiment 2				
Young	868 (142)	882 (168)	917 (156)	1054 (198)
Old	1284 (266)	1293 (305)	1373 (313)	1615 (431)

Table 3

*Mean reaction times (and standard deviations) in msec for each implicit trial type as a function of reported use of an explicit retrieval strategy in Experiment 1*

		Intact	Recombined	New
	<i>n</i>	Young Adults		
Explicit Strategy	12	967 (139)	1043 (147)	1152 (165)
No Explicit Strategy	24	970 (204)	1037 (195)	1086 (212)
		Old Adults		
Explicit Strategy	8	1405 (361)	1489 (238)	1580 (212)
No Explicit Strategy	16	1277 (303)	1402 (291)	1506 (429)

Table 4

*Mean reaction times (and standard deviations) in msec for each implicit trial type, and proportions of hits and false alarms to recombined and new pairs, as a function of reported use of an explicit retrieval strategy in Experiment 2*

		Intact	Recombined	New	Hits	FA (Rec)	FA (New)
	<i>n</i>	Young Adults					
Explicit Strategy	9	898 (124)	966 (163)	1134 (213)	.94 (.07)	.72 (.23)	.10 (.03)
No Explicit Strategy	23	856 (150)	898 (153)	1022 (182)	.89 (.13)	.64 (.19)	.07 (.14)
		Old Adults					
Explicit Strategy	11	1164 (218)	1254 (347)	1423 (379)	.93 (.11)	.89 (.12)	.09 (.03)
No Explicit Strategy	21	1346 (271)	1436 (282)	1716 (430)	.94 (.08)	.88 (.11)	.13 (.03)

*Note: Hit rate is the proportion of “old” responses given old status (i.e., correct responses to intact pairs). False alarm rate is the proportion of “old” responses given new status (i.e., incorrect responses to recombined pairs or to new pairs). Accuracy is the proportion of hits minus the proportion of false alarms.*

Table 5

*Proportions of hits to intact pairs, false alarms to recombined pairs, and false alarms to new pairs (and standard deviations) in Experiment 2*

	Hits	FA-Recombined	FA-New
Young	0.90 (.11)	0.66 (.20)	0.03 (.08)
Old	0.94 (.09)	0.88 (.11)	0.06 (.12)

*Note: Hit rate is the proportion of “old” responses given old status (i.e., correct responses to intact pairs). False alarm rate is the proportion of “old” responses given new status (i.e., incorrect responses to recombined pairs or to new pairs). Accuracy is the proportion of hits minus the proportion of false alarms.*



Table 6

*Effects of incidental and intentional encoding on proportions of hits and false alarms (and standard deviations) and on reaction times (and standard deviation) to intact, recombined, and new implicit trial types in Exp. 3*

	Recognition		
	Hits	FA-Recombined	FA-New
Incidental	0.89 (.15)	0.67 (.17)	0.05 (.17)
Intentional	0.89 (.14)	0.49 (.23)	0.04 (.16)
	Priming		
	Intact	Recombined	New
Incidental	856 (209)	933 (198)	1169 (381)
Intentional	994 (227)	985 (269)	1163 (290)

*Note: Hit rate is the proportion of “old” responses given old status (i.e., correct responses to intact pairs). False alarm rate is the proportion of “old” responses given new status (i.e., incorrect responses to recombined pairs or to new pairs). Accuracy is the proportion of hits minus the proportion of false alarms.*

Table 7

*Mean reaction times in milliseconds (and standard deviations) for each retrieval condition in Experiment 4*

	Same-Cue Condition		Reverse-Cue Condition	
	Studied	New	Studied	New
Young	784 (264)	918 (328)	1018 (285)	1087 (305)
Old	1060 (269)	1251 (280)	1281 (358)	1364 (346)

Table 8

*Mean reaction time in milliseconds (and standard deviation) for each retrieval condition in Experiment 5*

	Same-Cue Condition			Reverse-Cue Condition		
	Intact	Recombined	New	Intact	Recombined	New
Young	888 (184)	950 (273)	1081 (280)	1002 (212)	992 (250)	1137 (282)
Old	1154 (208)	1227 (271)	1515 (704)	1377 (286)	1394 (288)	1575 (305)

Table 9

*Mean reaction time (and standard deviation) in msec for the implicit retrieval conditions and mean proportions (and standard deviations) of hits, false alarms, and accuracy on the recognition test in Experiment 6*

		Retrieval Condition			
		Intact	Re-colored	Recombined	New
Speeded Classification	YA	864 (111)	877 (83)	907 (134)	1153 (238)
	OA	1021 (157)	1014 (171)	1076 (222)	1307 (335)
		Hit Rate	False Alarm Rate	Accuracy	
Associative Recognition	YA	.81 (.14)	.47 (.12)	0.34	
	OA	.80 (.14)	.66 (.24)	0.14	

*Note: Hit rate is the proportion of “old” responses given old status (i.e., correct responses to intact pairs). False alarm rate is the proportion of “old” responses given new status (i.e., incorrect responses to recombined pairs). Accuracy is the proportion of hits minus the proportion of false alarms.*

Table 10

*Priming effects (i.e., RT differences) in msec (and standard errors) across Exps 1-6*

Experiment	Group	Priming	
		Item	Assoc
Exp. 1	YA	69 (28)	70 (20)
	OA	100 (46)	111 (23)
Exp. 2	YA	137 (26)	40 (17)
	OA	242 (53)	90 (37)
Exp. 3	YA - Incidental	235 (56)	77 (29)
	YA - Intentional	178 (33)	-8.5 (47)
Exp 4	YA	Same cue (item only)	Reverse cue (item only)
	OA	134 (20)	69 (24)
		191 (19)	83 (41)
Exp. 5	YA	Item	
	OA	Same cue	Reverse cue
		131 (36)	104 (37)
		286 (41)	181 (41)
Exp. 5	YA	Assoc	
	OA	Same cue	Reverse cue
		69 (25)	-.02 (32)
		65 (30)	17 (38)
Exp. 6	YA	Item	Assoc
	OA	246 (43)	43 (17)
		230 (73)	55 (45)

Table 11  
*Regions of significance for contrasts of interest in young adults*

Contrast	Region of Activation	Hemisphere	BA	MNI Coordinates			t-value
				x	y	z	
Recombined>Intact	Medial Frontal Gyrus	R	6	12	26	62	8.05
	Middle Occipital Gyrus	L	19	-30	-80	2	5.66
	Middle Temporal Gyrus	L	21	-58	4	-14	4.66
	Superior Frontal Gyrus	L	6	-14	10	68	4.51
	Medial Frontal Gyrus	R	6	18	10	54	4.32
	Inferior Frontal Gyrus	L	44	-50	4	16	4.1
	Posterior Cingulate	R	29	10	-40	16	3.98
	Insula	R	13	50	6	6	3.86
	Inferior Frontal Gyrus	L	47	-34	40	-14	3.84
	Superior Temporal Gyrus	L	22	-66	-46	20	3.7
	Insula	L	13	-42	4	4	3.64
	Inferior Frontal Gyrus	L	47	-22	38	-4	3.57
	Medial Frontal Gyrus	R	6	8	2	60	3.5
	Middle Frontal Gyrus	L	9	-36	32	38	3.27
	Inferior Frontal Gyrus	L	47	-42	20	-4	3.21
Re-colored>Intact	Superior Frontal Gyrus	R	6	12	26	62	5.43
	Parahippocampal Gyrus	L	35	-18	-12	-18	4.61
	Amygdala	L	n/a	-22	-8	-12	4.57
	Superior Frontal Gyrus	R	6	12	6	60	4.5
	Inferior Temporal Gyrus	R	20	46	10	-34	4.44
	Middle Occipital Gyrus	R	19	46	-82	-12	4.32
	Superior Frontal Gyrus	R	6	24	-4	60	4.24
	Inferior Temporal Gyrus	L	21	-60	2	-18	4.14
	Inferior Frontal Gyrus	L	47	-48	18	4	4.07
	Superior Parietal Lobule	R	7	26	-60	68	4.05
	Middle Frontal Gyrus	L	9	-30	30	42	3.87
	Middle Frontal Gyrus	R	8	32	28	44	3.79
	Angular Gyrus	R	39	50	-72	28	3.64
	Inferior Temporal Gyrus	R	20	48	4	-28	3.61
	Inferior Frontal Gyrus	R	47	34	36	2	3.57
	Cingulate Gyrus	R	30	30	-50	6	3.46
	Inferior Frontal Gyrus	L	47	-56	30	-6	3.42
	Superior Parietal Lobule	R	7	16	-60	72	3.4
	Middle Occipital Gyrus	R	19	32	-92	6	3.39
	Inferior Frontal Gyrus	L	47	-26	18	-16	3.29

	Superior Frontal Gyrus	L	9	-10	52	32	3.29
New>Recombined	Superior Temporal Gyrus	L	41	-50	-30	14	6.4
	Middle Occipital Gyrus	R	19	38	-46	0	5.85
	Postcentral Gyrus	R	2	40	-24	32	5.28
	Middle Temporal Gyrus	L	21	-66	-30	2	5.06
	Postcentral Gyrus	R	40	58	-28	20	4.82
	Middle Frontal Gyrus	L	6	-30	-12	42	4.75
	Transverse Temporal Gyrus	R	42	60	-14	16	4.66
	Cingulate Gyrus	R	24	8	-4	32	4.55
	Paracentral Lobule	R	5	24	-44	48	4.41
	Amygdala	L	n/a	-36	2	-20	4.22
	Precentral Gyrus	L	6	-40	-10	56	4.21
	Superior Temporal Gyrus	R	22	56	-26	0	4.09
	Superior Frontal Gyrus	L	6	-12	-4	70	4.02
	Insula	L	13	-30	-8	26	3.89
	Inferior Temporal Gyrus	R	20	48	-8	-34	3.87
	Cuneus	L	7	-12	-70	28	3.86
	Cingulate Gyrus	L	24	-4	-4	36	3.8
	Medial Frontal Gyrus	R	6	52	-12	34	3.78
	Superior Temporal Gyrus	R	41	40	-32	14	3.63
	Precentral Gyrus	R	4	30	-28	74	3.62
	Inferior Temporal Gyrus	L	20	-46	4	-46	3.56
	Middle Temporal Gyrus	L	21	-50	10	-16	3.51
	Medial Frontal Gyrus	R	6	2	-8	68	3.44
	Medial Frontal Gyrus	L	10	-14	50	10	3.4
	Precuneus	R	7	12	-44	52	3.37
	Middle Occipital Gyrus	L	19	-34	-40	-6	3.28
	Inferior Temporal Gyrus	R	20	42	14	-42	3.23
	Anterior Cingulate Gyrus	L	24	-12	-22	38	3.2
Hits>Correct Rejections	Superior Temporal Gyrus	R	22	40	-58	12	4.04
	Inferior Frontal Gyrus	R	11	14	46	-18	3.79
	Precuneus	R	7	8	-74	36	3.59
	Inferior Frontal Gyrus	L	47	-34	26	-10	3.54

*Note: Regions significant at uncorrected  $p < .005$  with a cluster extent threshold of  $k > 5$ . R, right; L, left; BA, approximate Brodmann area based on coordinates.*

Table 12  
Regions of significance for contrasts of interest in older adults

	Region of Activation	Hemisphere	BA	MNI Coordinates			t-value
				x	y	z	
<i>Recombined&gt;Intact</i>	Middle Frontal Gyrus	L	11	-24	34	-18	4.98
	Superior Parietal Lobule	R	7	38	-72	52	4.77
	Medial Frontal Gyrus	R	10	4	58	-2	4.66
	Middle Frontal Gyrus	L	9	-26	22	36	4.56
	Superior Frontal Gyrus	L	10	-18	64	14	4.49
	Inferior Frontal Gyrus	L	45	-60	20	4	4.17
	Cuneus	R	17	12	-92	6	3.98
	Middle Temporal Gyrus	R	39	40	-76	26	3.95
	Middle Frontal Gyrus	L	10	-34	46	8	3.84
	Precuneus	L	7	-24	-76	52	3.71
	Posterior Cingulate	R	29	8	-38	14	3.63
	Fusiform Gyrus	L	37	-46	-56	-16	3.58
	Precuneus	R	31	16	-50	36	3.47
<i>Re-colored&gt;Intact</i>	Cingulate Gyrus	R	23	10	-28	28	6.10
	Cingulate Gyrus	L	31	-18	-58	26	4.93
	Cingulate Gyrus	L	31	-10	-42	34	3.47
	Cuneus	L	19	-10	-82	32	3.60
	Insula	L	13	-34	-42	18	8.47
	Insula	L	13	-30	-30	24	4.07
	Insula	R	13	38	-20	20	3.42
	Lingual Gyrus	L	18	-10	-56	4	4.58
	Middle Occipital Gyrus	R	19	30	-82	18	4.08
	Middle Temporal Gyrus	R	39	38	-68	20	3.50
	Postcentral Gyrus	L	40	-52	-28	18	4.68
	Postcentral Gyrus	R	3	30	-40	50	3.70
	Precentral Gyrus	R	6	44	-8	36	3.65
	Precentral Gyrus	R	6	52	-8	42	3.41
	Precuneus	R	39	44	-72	32	4.99
	Precuneus	L	31	-16	-68	24	4.27
	Superior Temporal Gyrus	R	22	66	-46	20	4.37
	Superior Temporal Gyrus	R	13	58	-42	18	3.26



<i>New&gt;Recombined</i>	Middle Frontal Gyrus	R	11	24	54	-10	6.96
	Precentral Gyrus	R	6	50	-6	24	4.85
	Postcentral Gyrus	L	43	-64	-16	22	4.66
<i>Hits&gt;Correct Rejections</i>	Precentral Gyrus	L	6	-38	-14	38	6.22
	Precentral Gyrus	L	6	-36	-12	40	4.22

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*Note: Regions significant at uncorrected  $p < .005$  with a cluster extent threshold of  $k > 5$ . R, right; L, left; BA, approximate Brodmann area based on coordinates.*

Table 13

*Regions of activation common to young and older adults*

Contrast	Region of Activation	Hemisphere	BA	MNI Coordinates			<i>t</i> -value
				x	y	z	
Recombined>Intact	Inferior Frontal Gyrus	L	44	-48	0	22	4.22
	Posterior Cingulate	R	29	8	-38	14	3.2
	Inferior Parietal Lobule	R	40	58	-48	50	3.03
	Insula	R	13	34	-42	20	2.47
	Precentral Gyrus	R	44	52	8	6	2.31
	Precentral Gyrus	L	44	-50	6	10	2.06
Re-colored>Intact	Angular Gyrus	R	39	48	-74	30	5.93
	Sub-Gyral	R	6	18	-8	56	4.23
	Hippocampus	L	n/a	-28	-38	2	4.15
	Middle Temporal Gyrus	L	39	-32	-60	22	4.07
	Precuneus	L	39	-36	-70	30	3.82
	Middle Temporal Gyrus	R	39	50	-72	20	3.53
	Postcentral Gyrus	R	3	30	-40	50	3.31
	Precuneus	L	31	-14	-66	24	3.27
	Hippocampus	L	n/a	-36	-6	-20	3.15
	Posterior Cingulate	L	30	-8	-54	12	2.89
	Inferior Frontal Gyrus	L	44	-48	0	18	2.84
	Middle Occipital Gyrus	L	19	-50	-56	-12	2.83
	Precuneus	L	31	-22	-70	20	2.69
	Posterior Cingulate	R	29	10	-44	16	2.66
	Superior Temporal Gyrus	L	22	-46	-38	2	2.6
	Lingual Gyrus	R	18	18	-80	-18	2.56
	Middle Occipital Gyrus	R	19	32	-90	10	2.54
	Cuneus	R	18	16	-90	22	2.49
	Cuneus	R	7	8	-70	32	2.39
	Middle Occipital Gyrus	R	18	44	-74	-18	2.38
	Precuneus	R	31	18	-66	26	2.33
	Superior Temporal Gyrus	R	39	40	-52	28	2.33
	Precuneus	L	19	-20	-86	36	2.3
	Precuneus	L	19	-26	-84	38	2.29
	Precuneus	L	19	-32	-78	32	2.27
	Parahippocampal Gyrus	L	28	-22	-12	-22	2.26
	Sub-Gyral	R	6	24	2	62	2.26
	Lingual Gyrus	R	17	14	-92	-14	2.25
	Middle Frontal Gyrus	R	8	26	36	42	2.25

	Middle Temporal Gyrus	L	21	-52	-46	6	2.17
	Hippocampus	L	n/a	-36	-26	-12	2.13
	Posterior Cingulate	R	31	14	-56	18	2.01
	Middle Frontal Gyrus	R	6	32	6	48	1.97
	Cingulate Gyrus	R	32	16	4	48	1.93
	Amygdala	R		26	6	-14	1.92
	Inferior Occipital Gyrus	L	18	-38	-80	-20	1.91
	Parahippocampal Gyrus	R	28	18	-8	-22	1.84
New>Recombined	Postcentral Gyrus	R	43	52	-10	20	5.35
	Anterior Cingulate	R	32	20	38	6	4.68
	Superior Parietal Lobule	L	7	-34	-66	46	4.34
	Postcentral Gyrus	L	1	-62	-18	24	4.21
	Anterior Cingulate	L	32	-16	44	12	4
	Precentral Gyrus	R	6	46	-10	28	3.96
	Cingulate Gyrus	L	23	-10	-30	30	3.9
	Postcentral Gyrus	R	40	56	-30	22	3.88
	Superior Frontal Gyrus	L	6	-20	-6	74	3.58
	Fusiform Gyrus	R	20	50	-12	-38	3.46
	Precentral Gyrus	L	4	-38	-18	46	3.37
	Superior Frontal Gyrus	L	9	-12	56	44	2.83
	Superior Frontal Gyrus	R	6	22	-6	76	2.76
	Superior Frontal Gyrus	L	6	-10	-6	72	2.72
	Parahippocampal Gyrus	R	36	30	-6	-38	2.54
	Postcentral Gyrus	L	3	-10	-36	72	2.53
	Superior Frontal Gyrus	R	6	12	-18	78	2.51
	Anterior Cingulate	L	32	-24	32	16	2.44
	Superior Frontal Gyrus	L	8	-12	48	48	2.33
	Superior Frontal Gyrus	L	10	-18	54	0	2.3
	Superior Frontal Gyrus	L	9	-20	48	42	2.29
	Precentral Gyrus	R	4	20	-30	74	2.28
	Postcentral Gyrus	L	3	-22	-34	76	2.21
	Precentral Gyrus	R	6	26	-24	74	2.18
	Middle Temporal Gyrus	R	21	38	12	-30	2
	Superior Temporal Gyrus	R	21	54	0	-10	1.95
	Precentral Gyrus	R	6	24	-20	78	1.92
Hits>Correct Rejections	Cingulate Gyrus	L	32	-10	24	34	2.21

*Note: Regions significant at uncorrected  $p < .005$  with a cluster extent threshold of  $k > 5$ . R, right; L, left; BA, approximate Brodmann area based on coordinates.*

Table 14  
*Regions more active in young than older adults*

	Region of Activation	Hemisphere	BA	MNI Coordinates			<i>t</i> -value
				x	y	z	
<i>Recombined&gt;Intact</i>	Superior Frontal Gyrus	R	6	12	26	62	4.99
	Middle Frontal Gyrus	L	11	-22	40	-2	4.78
	Superior Frontal Gyrus	R	9	20	42	40	4.14
	Medial Frontal Gyrus	R	6	18	8	56	4.12
	Middle Temporal Gyrus	L	21	-58	4	-16	3.51
	Middle Frontal Gyrus	R	10	30	46	6	3.27
	Inferior Frontal Gyrus	L	47	-42	22	-10	3.19
<i>Recolored&gt;Intact</i>	Superior Frontal Gyrus	R	6	10	26	60	5.81
	Superior Parietal Lobule	R	7	24	-62	68	4.87
	Medial Frontal Gyrus	L	9	-4	50	32	4.82
	Medial Frontal Gyrus	L	11	-10	54	-18	4.55
	Superior Frontal Gyrus	R	8	8	30	48	3.95
	Inferior Frontal Gyrus	L	47	-26	20	-16	3.67
	Superior Frontal Gyrus	R	6	10	6	62	3.54
	Medial Frontal Gyrus	R	6	16	8	56	3.52
	Superior Frontal Gyrus	R	9	4	50	36	3.47
	Inferior Parietal Lobule	R	40	42	-56	60	3.39
	Inferior Frontal Gyrus	L	47	-56	30	-2	3.37
	Superior Frontal Gyrus	R	8	18	36	56	3.24
	Medial Frontal Gyrus	L	6	-8	-30	60	3.15
	Anterior Cingulate	L	24	-14	18	22	3.11
	Superior Frontal Gyrus	R	9	12	52	40	2.86
<i>New&gt;Recombined</i>	Cingulate Gyrus	R	24	12	2	42	3.83
	Cingulate Gyrus	L	24	-10	2	44	3.19
	Cingulate Gyrus	R	24	4	-2	30	2.99
	Fusiform Gyrus	L	37	-46	-56	-14	3.37
	Inferior Frontal Gyrus	R	46	40	38	14	4.47
	Inferior Temporal Gyrus	R	20	56	-42	-12	3.26
	Medial Frontal Gyrus	R	9	10	40	28	3.62
	Middle Frontal Gyrus	L	6	-34	8	44	3.25
	Associative Visual Cortex	R	19	32	-44	-8	4.48
	Cingulate Gyrus	L	30	-32	-52	2	3.33
	Precentral Gyrus	L	6	-40	-6	42	3.11

	Precuneus	L	7	-8	-66	30	3.4
<i>Hits&gt;Correct Rejections</i>	Cingulate Gyrus	R	24	18	6	50	4.88
	Lingual Gyrus	L	18	-8	-68	2	4.38
	Fusiform Gyrus	R	20	46	-26	-16	4.29
	Lingual Gyrus	L	19	-28	-64	4	4.26
	Superior Temporal Gyrus	R	22	40	-58	12	4.24
	Precuneus	R	19	28	-80	32	4.06
	Superior Temporal Gyrus	R	22	50	-34	6	3.92
	Middle Frontal Gyrus	R	11	40	42	-16	3.87
	Inferior Frontal Gyrus	L	47	-38	30	-16	3.85
	Cuneus	R	7	8	-72	32	3.83
	Middle Temporal Gyrus	R	21	60	-34	-14	3.74
	Angular Gyrus	R	39	44	-64	32	3.68
	Insula	L	13	-42	-14	-10	3.65
	Superior Temporal Gyrus	R	39	52	-60	30	3.65
	Inferior Frontal Gyrus	L	47	-40	20	-6	3.61
	Superior Temporal Gyrus	R	22	50	8	4	3.61
	Inferior Frontal Gyrus	L	47	-26	28	-14	3.48
	Inferior Frontal Gyrus	R	47	38	22	-4	3.35
	Middle Temporal Gyrus	R	21	56	-28	-10	3.28
	Precentral Gyrus	R	44	48	10	12	3.27
	Inferior Frontal Gyrus	R	47	48	28	-6	3.26
	Precuneus	L	7	-4	-66	30	3.25
	Inferior Temporal Gyrus	L	20	-48	-16	-16	3.20
	Superior Temporal Gyrus	R	38	48	20	-12	3.20
	Inferior Frontal Gyrus	L	13	-34	20	-14	3.10
	Inferior Frontal Gyrus	R	47	30	28	-6	3.02
	Superior Temporal Gyrus	R	38	58	10	-6	3.00
	Cingulate Gyrus	R	31	8	-62	30	2.94

*Note: Regions significant at uncorrected  $p < .005$  with a cluster extent threshold of  $k > 5$ . R, right; L, left; BA, approximate Brodmann area based on coordinates.*

Table 15  
Regions more active in older than young adults

	Region of Activation	Hemisphere	BA	MNI Coordinates			t-value
				x	y	z	
<i>Recombined&gt;Intact</i>	Parahippocampal Gyrus	R	19	38	-46	-8	3.55
	Middle Frontal Gyrus	L	10	-34	48	8	3.53
	Fusiform Gyrus	R	20	54	-8	-26	3.52
	Cuneus	L	19	-10	-80	32	3.46
	Middle Frontal Gyrus	L	10	-30	44	18	3.46
	Lingual Gyrus	R	18	34	-72	-10	3.37
	Inferior Occipital Gyrus	L	18	-36	-82	-8	3.3
	Insula	R	13	36	6	16	3.24
	Fusiform Gyrus	L	37	-46	-58	-14	3.23
	Cingulate Gyrus	L	24	-14	-2	42	3.2
	Parahippocampal Gyrus	L	30	-30	-56	-2	3.2
	Superior Frontal Gyrus	L	10	-20	60	-2	3.19
	Lingual Gyrus	L	19	-16	-62	-8	3.17
	Cingulate Gyrus	L	32	-14	30	30	3.14
	Middle Frontal Gyrus	L	9	-52	28	34	3.14
	Insula	L	13	-30	-26	26	3.09
	Inferior Parietal Lobule	R	40	46	-60	46	3.05
	Superior Occipital Gyrus	R	19	36	-80	26	3.02
	Cuneus	L	7	-10	-72	30	2.96
	Precuneus	R	7	10	-80	52	2.94
<i>Re-colored&gt;Intact</i>	Cuneus	L	19	-8	-84	32	4.05
	Cuneus	L	18	-4	-88	10	3.33
	Inferior Occipital Gyrus	R	19	38	-70	-4	3.28
	Insula	L	13	-32	-42	18	3.96
	Insula	R	13	30	-26	24	3.77
	Insula	L	13	-36	-26	28	3.55
	Insula	R	41	34	-28	10	3.46
	Lingual Gyrus	R	19	20	-56	-4	3.07
	Middle Occipital Gyrus	R	19	28	-84	14	4.16
	Parahippocampal Gyrus	R	28	18	-4	-30	3.26
	Parahippocampal Gyrus	R	36	32	-8	-38	3.07
	Posterior Cingulate	L	30	-16	-56	18	3.62
	Superior Temporal Gyrus	R	22	66	-50	20	3.19

<i>New&gt;Recombined</i>	Superior Temporal Gyrus	R	22	38	-54	8	3.31
<i>Hits&gt;Correct Rejections</i>	Cingulate Gyrus	L	31	-22	-24	44	3.66
	Precentral Gyrus	L	6	-34	-12	32	3.27
	Middle Frontal Gyrus	L	10	-30	42	20	3.24
	Inferior Frontal Gyrus	L	45	-58	26	16	3.20
	Anterior Cingulate	L	32	-12	28	24	3.17
	Superior Parietal Lobule	L	7	-16	-68	64	3.08

*Note: Regions significant at uncorrected  $p < .005$  with a cluster extent threshold of  $k > 5$ . R, right; L, left; BA, approximate Brodmann area based on coordinates.*

Table 16

*Hypothesized MTL regions elicited as conceptual associative activations and perceptual associative deactivations*

		Region of Activation	Hemisphere	BA	MNI Coordinates			<i>t</i> -value
					x	y	z	
<i>Intact&gt;Recombined</i>	YA	Hippocampus	L	n/a	-30	0	-22	1.83
		Hippocampus	R	n/a	30	-20	-8	1.81
		Parahippocampal Gyrus	R	28	20	-4	-30	1.80
		Parahippocampal Gyrus	L	36	-44	-28	-14	1.71
	OA	Hippocampus	L	n/a	-32	-6	-14	3.46
		Parahippocampal Gyrus	R	28	22	-8	-24	1.91
<i>Re-colored&gt;Intact</i>	YA	Parahippocampal Gyrus	L	35	-18	-12	-18	4.61
		Hippocampus	L	n/a	-38	-4	-18	3.43
		Parahippocampal Gyrus	R	28	20	-8	-22	2.01
	OA	Parahippocampal Gyrus	L	34	-12	6	-16	2.62
		Parahippocampal Gyrus	R	35	18	-42	0	2.47

*Note: Regions significant at uncorrected  $p < .05$  with a cluster extent threshold of  $k > 10$ . R, right; L, left; BA, approximate Brodmann area based on coordinates.*



Table 17

*Hypothesized regions of activation associated with successful explicit relational retrieval*

	Region of Activation	Hemisphere	BA	MNI Coordinates			<i>t</i> -value
				x	y	z	
YA	Inferior Parietal Lobule	R	40	60	-52	44	2.9
	Fusiform Gyrus	R	37	38	-34	-8	2.6
	Inferior Parietal Lobule	R	40	50	-62	50	2.35
	Middle Frontal Gyrus	R	9	34	18	38	2.26
	Middle Frontal Gyrus	R	46	54	26	30	2.22
	Hippocampus	R	n/a	28	0	-26	2.2
OA	Precuneus	L	7	-6	-68	44	2.80
	Precuneus	R	7	10	-70	36	2.70
	Inferior Parietal Lobule	L	40	-32	-42	36	2.69
	Inferior Frontal Gyrus	L	11	-18	46	-20	2.27
	Inferior Parietal Lobule	R	40	68	-36	36	2.15
	Middle Frontal Gyrus	L	47	-44	40	4	1.96
	Medial Frontal Gyrus	R	11	4	44	-16	1.95

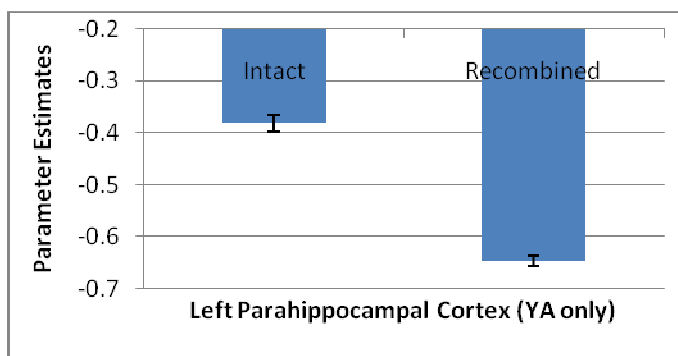
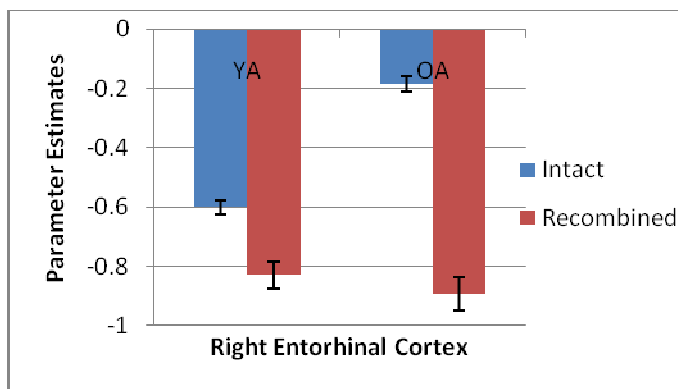
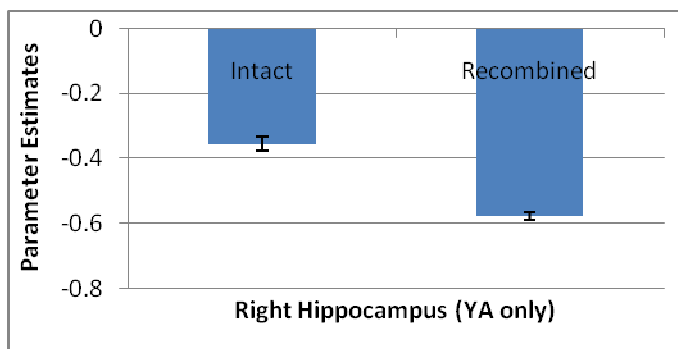
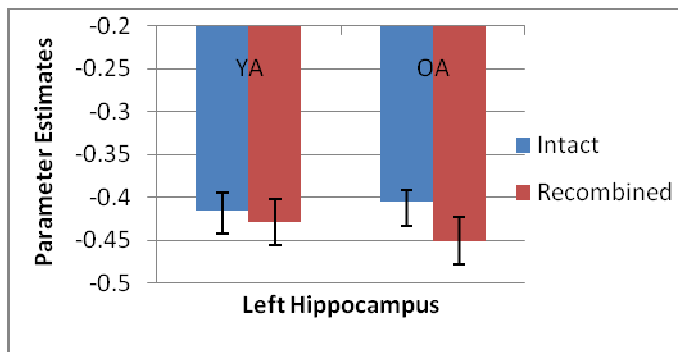
*Note: Regions significant at uncorrected  $p < .05$  with a cluster extent threshold of  $k > 10$ . R, right; L, left; BA, approximate Brodmann area based on coordinates.*

Table 18  
*Hypothesized frontal regions more active in OAs than YAs*

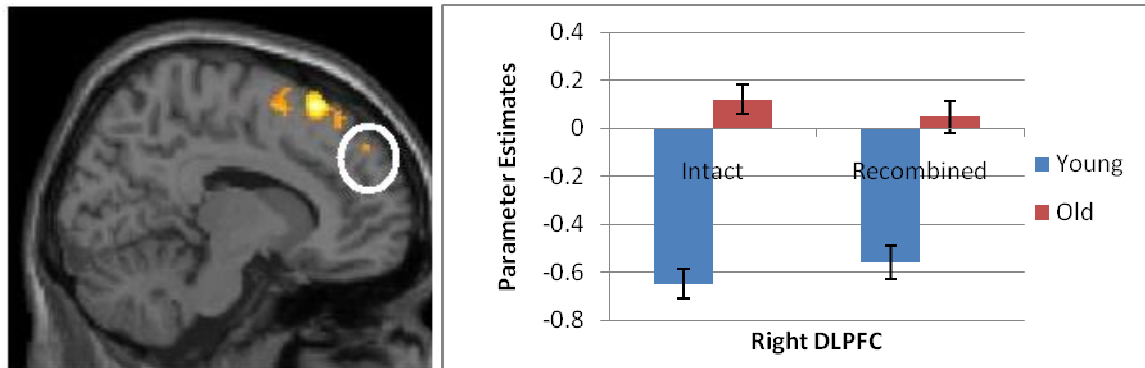
Contrast	Region of Activation	Hemisphere	BA	MNI Coordinates			<i>t</i> -value
				x	y	z	
Intact>Recombined	Middle Frontal Gyrus	L	11	-22	40	-2	4.78
	Superior Frontal Gyrus	R	9	20	42	40	4.14
	Middle Frontal Gyrus	R	10	30	46	6	3.27
	Inferior Frontal Gyrus	L	47	-42	22	-10	3.19
Intact>Re-colored	Medial Frontal Gyrus	L	11	-10	54	-18	4.55
	Inferior Frontal Gyrus	L	47	-26	20	-16	3.67
	Inferior Frontal Gyrus	L	47	-56	30	-2	3.37
	Medial Frontal Gyrus	L	9	-4	50	32	4.82
	Superior Frontal Gyrus	R	9	4	50	36	3.47
	Superior Frontal Gyrus	R	9	12	52	40	2.86
Recombined>New	Medial Frontal Gyrus	R	9	10	40	28	3.62
	Inferior Frontal Gyrus	R	46	40	38	14	4.47
Hits>Correct Rejections	Middle Frontal Gyrus	L	10	-30	42	20	3.24
	Inferior Frontal Gyrus	L	45	-58	26	16	3.20

*Note: Regions significant at uncorrected  $p < .005$  with a cluster extent threshold of  $k > 5$ . R, right; L, left; BA, approximate Brodmann area based on coordinates.*

*Figure 1.* Parameter estimates in medial temporal regions that were more active during intact than recombined trials.

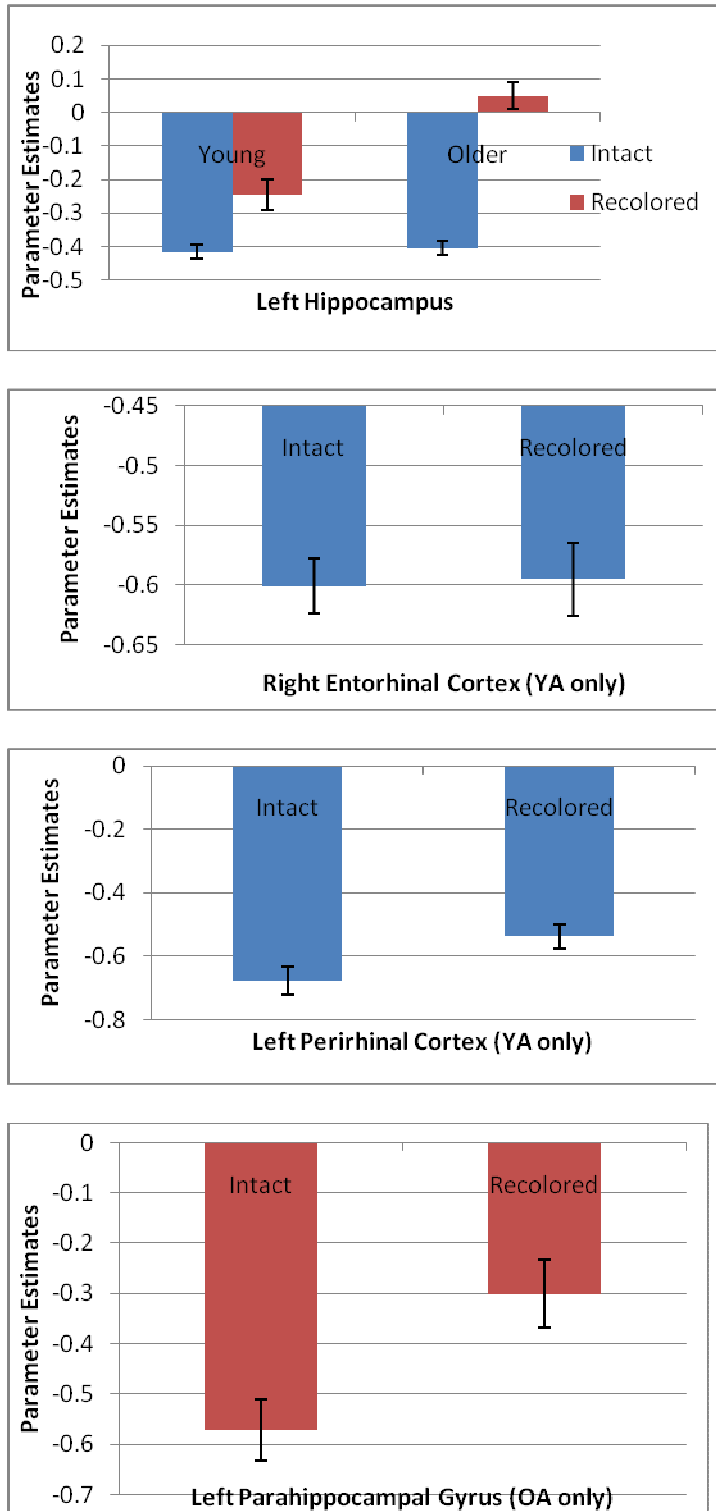


*Figure 2. Regions more active in older than young adults during intact relative to recombined trials.*

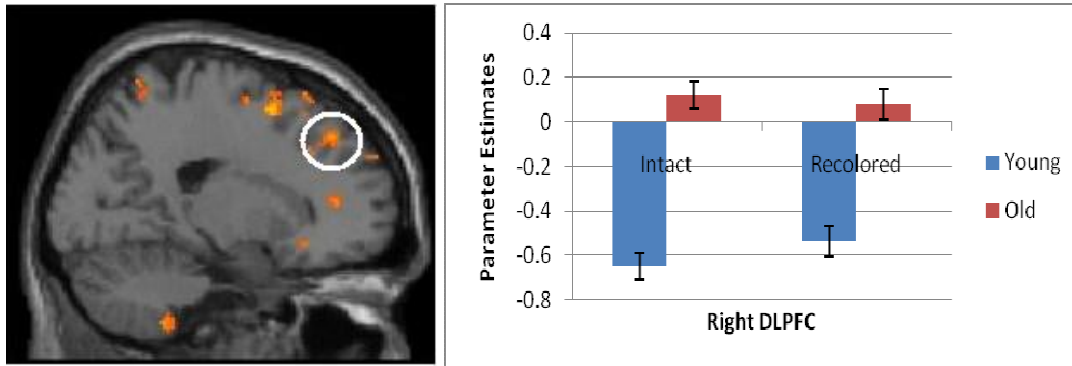


*Note: Statistically significant activity is superimposed onto a canonical single-subject anatomical T1 image. Circled area corresponds to right dorsolateral PFC in BA 9 (coordinates 20, 42, 40 in MNI space).*

Figure 3. Parameters estimates in medial temporal regions that were more active during re-colored than intact trials.



*Figure 4.* Regions more active in older than younger adults during intact relative to re-colored trials.



*Note:* Statistically significant activity is superimposed onto a canonical single-subject anatomical T1 image. Circled area corresponds to right dorsolateral PFC in BA 9 (coordinates 12, -52, 40 in MNI space).