Episodic Memory Decline in Healthy Ageing

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Declaration

This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others.

The experiment presented in Chapter 2 was reported in the paper by Alexandra N. Trelle, Richard, N. Henson, & Jon, S., Simons (2015). Identifying age-invariant and age-limited mechanisms for enhanced memory performance: Insights from self-referential processing in younger and older adults. *Psychology and Aging, 30,* 324-333.

The experiments presented in Chapter 3 were reported in the paper by Alexandra N. Trelle, Richard, N. Henson, & Jon, S., Simons (under review). Declines in representational quality and strategic retrieval processes contribute to age-related increases in false recognition.

I hereby state that this dissertation does not exceed 60,000 words, and thus is within the word limit specified by the Degree Committee for the Faculty of Biology.

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Abstract

Age-related decline in episodic memory is characterised by a disproportionate reduction in the ability to retrieve specific details of previously experienced events with minimal support from external cues. Two factors that feature prominently in accounts of age-related memory impairment include a reduction in the specificity with which older adults encode or represent event details, and declines in the ability to engage controlled retrieval processes. The goal of this thesis is to evaluate the contribution of these two factors to age differences in memory performance across three distinct paradigms. These paradigms vary in how episodic memory is operationalized, but make common demands on controlled and deliberate retrieval of specific details of previously experienced events.

The results of Chapters 2 and 3 provide evidence that enhancing the quality of stimulus representations at encoding, or minimizing demands on strategic control processes during retrieval, do not eliminate age differences in performance when each manipulation is implemented individually. However, the combination of environmental support at both encoding and retrieval did reduce age-related impairment in memory performance across two different experimental paradigms, providing evidence that ageing is typically characterized by declines in both of these factors. Moreover, neuropsychological profiles of older adults described in Chapter 3 provided evidence for separable relationships between memory performance and measures of representational quality and strategic retrieval processes. Together, these findings implicate the involvement of multiple factors in age-related memory decline, and provide indirect evidence that individual differences in these factors reflect alterations in brain structure and function.

Chapter 4 sought neural evidence for age differences in representational quality and strategic retrieval processes using pattern similarity analysis of fMRI data. The results revealed age-related declines in the differentiation of neural representations in ventral visual cortex during encoding of word-picture pairs, as well as age-related reductions in the specificity of cortical reinstatement during associative recognition. In particular, whereas younger adults exhibited event-specific reinstatement of encoding-related activity during retrieval, suggesting the use of a recollection-based retrieval strategy, older adults did not. Instead, older adults exhibited neural activity patterns more consistent with a reliance on cue familiarity as opposed to recollection, which could not be accounted for by age differences at encoding. Together, these results provide evidence for separable contributions of representational quality and strategic retrieval processes to age-related declines in episodic memory.

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Chapter 1

Introduction

Aging is associated with declines in a variety of different cognitive, sensory, and motor functions, but reductions in memory ability are among the most prominent and concerning deficits experienced by older individuals. However, memory is not a unitary construct, and not every aspect of memory is affected in a similar way by aging. In particular, long-term memory is thought to be divisible into separable, yet interacting memory systems that include episodic memory, semantic memory, and procedural memory (Tulving, 1987). Evidence from both cross-sectional and longitudinal studies suggests that *Semantic Memory*, memory for general facts and decontextualized knowledge, and *Procedural Memory*, experience-related changes in behaviour that are expressed automatically in the absence of conscious awareness, can be maintained throughout much of the lifespan (Nyberg, Backman, Erngrund, Olofsson, & Nilsson, 1996; Park et al., 2002; Nilsson, 2003). In contrast *Episodic Memory*, memory for personally experienced events that are bound to a particular time and place, often begins to decline dramatically at around 60 years of age (Nyberg et al., 1996; Park et al., 2002; Nilsson, 2003). The primary goal of this thesis is to further characterise the factors underlying age-related declines in episodic memory. To do so, it is important to first identify the patterns of behavioural and neurobiological change associated with memory decline in healthy aging.

In particular, age-related changes in episodic memory are not ‘all-or-none’, such that older adults simply cannot remember past experiences, or recall fewer experiences than younger adults. Instead, aging is thought to affect the quality of one’s memory, reducing the ability to recollect rich and detailed accounts of past experiences, but leaving memory for more general aspects, or ‘the gist’ of previous events relatively intact (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). For example, older adults typically report finding it increasingly difficult to recall someone's name, even when they can recognize their face, or find that they can remember hearing a fact, but not recall where or from whom they heard it. Such anecdotal reports of memory difficulties among older adults have received much support from evidence obtained through laboratory-based tests of episodic memory. These tests typically probe memory for events created in the context of the experimental session, rather than events from one's personal past. Although these experiments come in many different forms and tend to vary substantially with respect to both the stimuli to be remembered (e.g., words, pictures, paired associates), and the way in which memory is tested (e.g., recall, item recognition, associative recognition), a rather consistent pattern has emerged across experiments. In particular, older adults tend to exhibit a decline in the ability to recover specific event details, but display relatively intact memory for more general aspects of previous events (Craik, 1994; Schacter, Koutstaal, & Norman, 1997).

It is important to note that this pattern of episodic memory impairment among older adults has often been described as an impairment in recollection, coupled with preserved familiarity (Yonelinas, 2002). Whereas recollection describes the retrieval of qualitative aspects of a previous experience, including specific perceptual and contextual details, familiarity describes a fairly rapid and automatic feeling of knowing that a stimulus has been encountered previously (Mandler, 1980; Jacoby, 1991). Although the phenomenological experience associated with each of these processes is consistent with that which older adults experience, and indeed fits much of the existing data, this simple distinction does not account for the full range of deficits exhibited by older adults, and will not be adopted here. Thus, the terms recollection and familiarity will be used throughout this thesis to describe existing evidence in the literature and to relate current findings to previous work, but they are not useful for explaining the pattern of age-related memory deficits explored here. Instead, the characterization of age-related memory impairment in the current thesis is that of a decline in memory for specific event details, coupled with intact memory for the general aspects of previous experiences.

The experiments that comprise this thesis aim to provide further insights into the underlying mechanisms contributing to the pattern of age-related decline in episodic memory. To investigate this question, I will focus on three different experimental paradigms that have been used extensively to investigate age differences in episodic memory, which reliably detect substantial age differences in performance, and which exemplify common memory errors experienced by older adults. These include impairments in the ability to recall specific information from previous events in the absence of external cues (e.g., the items on your grocery list that was left at home), reductions in memory for associations between items (e.g., the name of the individual you met at a friend’s Christmas party), and declines in the ability to distinguish between highly similar events (e.g., where you parked your car yesterday versus the day before).

Although these three illustrations of age-related memory impairment might appear dissimilar on the surface, the underlying mechanisms associated with these memory errors may be highly overlapping. In particular, a number of cognitive operations and neuroanatomical substrates may be common to each of these different phenomenological experiences of memory decline, a possibility that will be explored throughout this thesis. In the following sections, I will first describe the neural basis of episodic memory, and the age-related changes in brain structure and function that are thought to contribute to episodic memory decline among older adults. I will then describe the typical behavioural and neurobiological profile of age-related declines in the ability to i) recall event details in the absence of external cues, ii) remember associations between items, and iii) discriminate between similar events. Finally, I will propose a two-factor theory that may account for the full range of observations, and go on to test this hypothesis across three different experimental paradigms that assess the effects of age on recall, associative memory, and mnemonic discrimination.

The Neural Basis of Episodic Memory

Studies of amnesiac patients with focal lesions (Scoville & Milner, 1957) and animal models of amnesia (Mishkin, 1978) have identified the medial temporal lobe (MTL) as critical for supporting the formation and retrieval of new episodic memories (see Squire, Stark, & Clark, 2004; Eichenbaum, Yonelinas, & Ranganath, 2007). This region is comprised of multiple structures, including the hippocampus and adjacent entorhinal, perirhinal, and parahippocampal cortices, which are each thought to make different contributions to episodic memory. There is much debate surrounding the functional organization of the MTL (see Ranganath, 2010 for review), of which an in depth discussion is beyond the scope of this thesis. However, anatomical studies across species have identified a hierarchical organization within this region, such that the hippocampus receives input from the entorhinal, perirhinal, and parahippocampal cortical regions, which themselves receive input from sensory neocortical regions throughout the brain (Burwell, 2000). In particular, the perirhinal cortex is thought to receive inputs from ventral cortical regions (e.g., striate, prestriate, & inferior temporal cortex) and support representations of item information (e.g., faces, objects), whereas the parahippocampal cortex is thought to receive inputs from dorsal cortical regions (e.g., striate, prestriate, and inferior parietal cortex) and support the representation of context information (e.g., spatial location; Mishkin, Ungerleider, & Macko, 1983). These two streams of input converge in the hippocampus via the lateral and medial entorhinal cortex, respectively (Burwell, 2000; Maas, Berron, Libby, Ranganath, & Duzel, 2015).

Consistent with this hierarchical structure, dominant views of MTL organization propose that the perirhinal and parahippocampal cortices support memory for item and context information, respectively, whereas the hippocampus performs relational binding of these event elements into a unique representation (Cohen & Eichenbaum, 1993; Eacott & Norman, 2004; Diana, Yonelinas, & Ranganath, 2007). Evidence for this idea has come from functional neuroimaging studies in humans identifying selectivity in the neural responses of the perirhinal cortex to faces and objects, and the parahippocampal cortex to both spatial and non-spatial context (Staresina, Duncan, & Davachi, 2011; Diana, Yonelinas, & Ranganath, 2012; Liang, Wagner, & Preston, 2013). Similarly, lesion studies in rodents and monkeys have demonstrated selective deficits in object and context memory following perirhinal and postrhinal lesions, respectively (Gaffan, Healey, & Eacott, 2004; Norman & Eacott, 2005).

These anatomical dissociations between the types of information supported by hippocampal and extra-hippocampal structures have also led to the proposal that the medial temporal lobes are not a dedicated long-term memory system, but rather contribute to short-term/working memory and perception for complex object, spatial, and relational stimuli (Bussey & Saksida, 2007; Graham, Barense, & Lee, 2010). Evidence for this idea comes from neuroimaging studies identifying the involvement of medial temporal lobe regions during perceptual tasks that include their preferred stimulus type (Barense, Henson, Lee, & Graham, 2010), as well as stimulus-specific deficits in complex perception in patients (Barense et al., 2005; Barense, Gaffan, & Graham, 2007; Lee et al., 2007) and animals (Bussey, Saksida, & Murray, 2002; Bussey, Saksida, & Murray, 2003) with MTL lesions. In addition to this representational view of MTL specialization, process-based distinctions have also been proposed. In particular, dual process models of MTL function suggest that the hippocampus is critical for recollection, whereas surrounding cortical regions can support familiarity (Brown & Aggleton, 2001; Eichenbaum et al., 2007). However, the benefits of adopting a process-based division of the MTL over a representational view has been challenged (Bussey & Saksida, 2007; Cowell, Bussey, & Saksida, 2010), a topic that will be examined later in this thesis.

Beyond the MTL, another region that has been critically implicated in episodic memory is the prefrontal cortex (Moscovitch, 1992; Simons & Spiers, 2003). In contrast to patients with MTL damage, who typically exhibit profound anterograde amnesia, individuals with focal lesions of the prefrontal cortex often present with a very different pattern of deficits that may include impairments of executive function, such as selective attention, inhibitory control, working memory, and cognitive flexibility (Stuss & Benson, 1984; see Alvarez & Emory, 2006 for review). Further study of these individuals has led to observations of specific memory deficits including elevated rates of false recognition accompanied by high levels of confidence (Parkin, Bindschaedler, Harsent, & Metzler, 1996; Schacter, Curran, Gallucio, Miberg, & Bates, 1996), impaired memory for the source and temporal context in which information was initially encountered (Johnson, O’Connor, & Cantor, 1997; Janowsky, Shimamura, & Squire, 1989), and disproportionate deficits in free recall relative to recognition (Parkin, Yeomans, & Bindschaedler, 1994; Wheeler, Stuss, & Tulving, 1995).

Such observations led to the proposal that the prefrontal cortex is critical for supporting cognitive control processes that contribute to organizational, strategic, and goal-directed aspects of memory encoding and retrieval (Moscovitch, 1992; Simons & Spiers, 2003). During encoding, the prefrontal cortex is thought to be critical for organising and prioritising incoming information. The ventrolateral prefrontal cortex is thought to support selection and maintenance of retrieved information, as well as semantic elaboration (Badre & Wagner, 2007), whereas the dorsolateral prefrontal cortex is thought to support the manipulation and organization of information in working memory (Blumenfeld & Ranganath, 2007). During retrieval, the prefrontal cortex is thought to be critical for goal-directed search and post-retrieval evaluation processes. In particular, the ventrolateral prefrontal cortex has been linked to cue elaboration, phonological maintenance/rehearsal, and selection amongst competing representations, whereas the dorsolateral prefrontal cortex has been linked to monitoring and evaluation processes (Wagner, Maril, Bjork, & Schacter, 2001; Dobbins, Foley, Schacter, & Wagner, 2002).

Although the medial temporal lobes and prefrontal cortex are nodes of a broader network of brain regions that have been implicated in episodic memory retrieval, which also includes regions such as the lateral parietal cortex and retrosplenial cortex (Ranganath & Ritchey, 2012; Vilberg & Rugg, 2013), investigations of age-related memory decline have often focused on the former two areas. This emphasis has been driven both by observations that age-related memory deficits appear similar to those displayed by individuals with damage to the prefrontal and medial temporal lobes, as well as observations that these regions display perhaps the most dramatic age-related change. The following section will review existing evidence regarding the effects of age on the structure and function of these regions.

Age-related Changes in Brain Structure and Function

Although aging is associated with widespread neurobiological changes throughout the brain, evidence from both cross-sectional and longitudinal research suggests that the prefrontal cortex (PFC) is disproportionately affected by age (Buckner, 2004; Hedden & Gabrieli, 2004). For example, evidence suggests that PFC gray matter volume declines more rapidly than any other region of the brain (Raz et al., 1997), and that lateral regions of the PFC implicated in episodic encoding and retrieval exhibit the greatest decline (Tisserand et al., 2002). Relationships between gray matter volume decline and episodic memory performance have been identified, mediated by reductions in working memory and inhibitory control processes (Head, Rodrigue, Kennedy, & Raz, 2008). Moreover, functional neuroimaging studies have identified age differences in prefrontal function as measured by regional BOLD activity during encoding and retrieval. These changes are characterised by both under-recruitment (Logan et al., 2002; Nyberg et al., 2010) and over-recruitment (Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady, McIntosh, & Craik, 2005; Davis, Dennis, Daselaar, Fleck & Cabeza, 2008) of this region, as well as altered functional connectivity between the prefrontal cortex and other brain regions (Grady, McIntosh, & Craik, 2003; Dennis et al., 2008). These changes may arise, at least in part, due to decline in white matter integrity with age (Zhu, Johnson, Kim, & Gold, 2015), which are widespread throughout the brain, but most pronounced in the prefrontal cortex (Head et al., 2004).

A second region that has been identified as more vulnerable to the effects of age as compared to the rest of the brain is the medial temporal lobe (MTL) (Hedden & Gabrieli, 2004). Within this region, the hippocampus is sometimes thought to be affected to a greater degree than the surrounding cortical regions due to observations that declines in gray matter volume are greater than that observed in the entorhinal or parahippocampal cortex (Raz, Rodrigue, Head, Kennedy, & Acker, 2004; Raz et al., 2005). Indeed, the extent of hippocampal volume loss has been linked to episodic memory decline in older adults (Persson et al., 2011; Head et al., 2008). Moreover, age-related declines in regional BOLD activity in the hippocampus have been identified during both encoding and retrieval of episodic memories (Grady et al., 1995; Dennis et al., 2008). However, there is also evidence that not all hippocampal subregions, which include the dentate gyrus, CA1, CA3, and subiculum, are affected to the same extent by healthy aging (Small, Chawla, Buonocore, Rapp, & Barnes, 2004).

Existing evidence suggests that the dentate gyrus (DG) is particularly affected by age (Small et al., 2004), exhibiting greater volume loss than other subregions due to declines in synaptic density (West, 1993). Moreover, aging is associated with reductions in synaptic input to the DG from the entorhinal cortex due to declines in the perforant path integrity, the white matter tract that connects these regions, and these reductions have been related to behavioural measures of memory impairment in older adults (Yassa, Muftuler, & Stark, 2010; Bennett & Stark, 2015). Finally, evidence for functional alterations in the DG/CA3 network, characterised by hyperactivity of the CA3 auto-associative network, has also been identified in intracranial recordings in rodents (Wilson, Ikonen, Gallagher, Eichenbaum, & Tanila, 2005; El-Hayek et al., 2013) and high-resolution functional neuroimaging in humans (Yassa et al., 2011). These changes may arise, at least in part, due to reductions in modulatory input to the hippocampus by cholinergic, dopaminergic, and noradrenergic neurotransmitter systems (Leal & Yassa, 2015).

Although studies of age-related effects on MTL structure and function have often focused on the hippocampus, recent evidence suggests that the perirhinal cortex (PRC) and lateral entorhinal cortex (LEC) also exhibit age-related changes (Leal & Yassa, 2015). Although significant reductions in gray matter volume are not often observed in these regions in healthy aging (Rapp et al., 2002), there is some evidence for age-related dysfunction of these regions. For example, rodent studies have provided evidence for age-related changes in PRC neuron responsivity during object exploration (Burke, Hartzell, Lister, Hoang, & Barnes, 2012; Burke et al., 2014), as well as dysregulation of neurotransmission and cellular homeostasis in this region (Liu, Gupta, Jing, Y, & Zhang, 2008; Moyer, Furtak, McGann, & Brown, 2009). In humans, age-related reductions in PRC activity during perceptual discrimination of complex objects have been identified and linked with impaired performance (Ryan et al., 2012). However, there is also evidence to suggest that the LEC and PRC are among the first brain regions to be affected by Alzheimer's disease (AD) (Braak & Braak, 1991; Khan et al., 2014). Thus, it has been proposed that age effects on this region may not represent healthy aging, but rather be a signature of preclinical AD (Newsome et al., 2012; Yeung et al., 2014; but see Reagh et al., 2016). Evidence for this possibility is presently mixed, but is relevant to the current investigation and will be addressed in the final discussion chapter.

Outside of prefrontal and medial temporal lobe regions, age-related changes have also been observed in sensory processing regions in the ventral visual stream, including inferior occipital and inferior temporal cortices. Although these regions are not typically emphasised in studies of cognitive aging due to a relative preservation of gray matter volume compared to frontal and medial temporal regions (Raz et al., 2005), functional changes in these regions have been observed. In humans, functional neuroimaging evidence has identified reduced selectivity of neural responses in ventral visual cortex to visual stimuli from different stimulus categories (e.g., faces, objects, scenes; Park et al., 2004; Carp, Park, Polk, & Park, 2011; Burianova, Lee, Grady, & Moscovitch, 2013). Similarly, studies using fMRI adaptation have found that older adults exhibit less selective neural adaptation in response to both identical and similar exemplars within a given category, whereas younger adults selectively exhibit adaptation for identical exemplars (Goh, Suzuki, & Park, 2010). These observations have been complemented by single-neuron recordings in aged primates, which provide evidence for reductions in the selectivity of neural response tuning to different stimulus inputs in early (Schmolesky, Wang, Pu, & Leventhal, 2000; Leventhal, Wang, Pu, Zhou, & Ma, 2003) and late (Yu, Wang, Li, Zhou, & Leventhal, 2006; Liang et al., 2010) visual cortices. Taken together, these findings suggest that neural specialization and selectivity in visual cortical regions declines with age. Given that the ventral visual cortices are among regions that provide sensory input during memory encoding, these changes may also contribute to age-related declines in episodic memory.

The alterations in brain structure and function described above are thought to play important roles in the episodic memory impairments exhibited by older adults. In particular, these neural changes have been implicated in age-related deficits in free recall, associative memory, and mnemonic discrimination. In the next three sections, I will review behavioural evidence for each of these impairments and describe the corresponding neural changes typically exhibited by older adults in each of these paradigms.

Age Differences in Free Recall

One of the most robust and reliable findings in studies of age-related memory decline is impaired recall of single items, such as a list of common words. In such experiments, older adults typically recall significantly fewer items than younger adults (Burke & Light, 1981; Wingfield, Lindfield, & Kahana, 1998). Older adults are also more likely than younger adults to make intrusions from non-studied items during recall (Kahana, Howard, Zaromb, & Wingfield, 2002; Kahana, Dolan, Sauder & Wingfield, 2005). However, if memory for these stimuli is later additionally assessed by recognition tests, in which a mixture of studied items and novel items are provided as cues for retrieval, age differences in performance tend to be significantly reduced (Craik & McDowd, 1987). The observation that older adults are impaired at recalling previous events in the absence of external cues, but can often recognize these events when sufficient retrieval support is provided, has led to the proposal that aging is associated with a decline in the ability to carry out the controlled and strategic retrieval processes necessary to support free recall of previous event information.

In particular, recalling information in the absence of external cues necessitates control and coordination of multiple processes, including strategic and organised search, retrieval, and evaluation processes (Gershberg & Shimamura, 1995; Long, Oztekin, & Badre, 2010). In contrast, item recognition tests provide strong cues for retrieval (e.g., the studied items themselves), thereby enabling memory to be supported equally well by assessments of test-item familiarity, as by recollection of studied items (Mandler, 1980). Importantly, familiarity-based responding is thought to occur relatively automatically, based on increased perceptual or conceptual fluency for studied as compared to novel items, whereas recollection is thought to involve conscious and controlled retrieval of event details to support recognition decisions (Jacoby, 1991). Evidence for this idea has come from studies showing that dividing attention during retrieval decreases recollection, but leaves familiarity unaffected (Jacoby, Toth & Yonelinas, 1993). Thus, it has been proposed that aging is associated with a reduction in the ability to carry out controlled and strategic processes, whereas more automatic processes remain relatively unaffected (Jennings & Jacoby, 1993). Consistent with this idea, previous research measuring the contributions of recollection and familiarity to recognition decisions typically identifies age-related reductions in estimates of recollection, coupled with relatively stable estimates of familiarity with age (see Koen & Yonelinas, 2014 for review; but see Prull, Dawes, Martin, Rosenberg, & Light, 2006; Duarte, Graham, & Henson, 2010).

Age-related declines in the ability to initiate and carry out the controlled processes necessary to support recall, as compared to the more automatic processes that can support recognition, are consistent with age-related declines in frontal lobe function. In particular, the prefrontal cortex has been implicated in supporting the execution of organisational strategies during recall, including semantic clustering of related items, and temporal clustering of items presented contiguously during encoding (Gershberg & Shimamura, 1995; Long, Oztekin, & Badre, 2010). Age-related declines in the use of these strategies, illustrated by reductions in category and temporal clustering (Wingfield et al., 1998), have been related to individual differences in frontal lobe function, with higher frontal function associated with better recall performance and greater clustering evidence (Taconnat et al., 2009). Similarly, in tests of recognition, older adults who perform more poorly on measures of frontal lobe function exhibit a greater reliance on familiarity (Parkin & Walter, 1992; Davidson & Glisky, 2002). Age-related declines in prefrontal function have also been identified in neuroimaging studies that observe reductions in the engagement of this region in older adults during conditions of goal-directed, strategic retrieval (Morcom & Rugg, 2004; Velanova, Lustig, Buckner, Jacoby, & Buckner, 2007).

A second factor that may contribute to age-related declines in recall, relative to recognition, is a decline in the quality of event representations with age. In particular, poor encoding could have a knock-on effect of leaving fewer event details available for retrieval, as well as making stored details more difficult to retrieve in the absence of retrieval support. In support of this idea, older adults' ability to recall information from previous events (e.g., a list of stimuli) is significantly improved when the stimuli to be remembered are more distinctive. For example, when participants study pictures instead of words, older adults exhibit significant enhancements in recall performance (Craik & Byrd, 1982; Park, Puglisi, & Smith, 1986; Luo, Hendriks, & Craik, 2007). This enhancement is thought to arise because pictures are more distinctive stimuli as compared to words, resulting in a more elaborative memory trace that is easier to retrieve in the absence of retrieval cues. The substantial benefits to recall performance gained by older adults following such a manipulation suggest that event representations become less distinctive with age.

One possible explanation for age-related reductions in event distinctiveness is that older adults are less likely to spontaneously initiate elaborative encoding of new information, resulting in impoverished or generic memory traces (Craik & Rose, 2012). In support of this idea, age differences in recall tend to be largest under intentional encoding conditions, when participants must come up with their own strategies for optimally encoding new information (Craik & Byrd, 1982). Moreover, when given more time under such intentional conditions, younger, but not older, adults exhibit improvements in memory performance, suggesting older adults are less likely to use this time to engage in more elaborative encoding unprompted (Craik & Rabinowitz, 1985; Rabinowitz, 1989). In contrast, when provided with more guided forms of elaboration, older adults can often benefit as much as younger adults, and exhibit significant improvements in recall performance. For example, providing an orienting task that facilitates deep and meaningful stimulus processing, such as making semantic judgments on words during encoding, can benefit older adults' performance as much as younger adults (Craik & Byrd, 1982; Logan et al., 2002). Similarly, when participants are asked to generate study items from word fragments, as compared to simply reading complete words, recall is substantially enhanced in both older and younger adults (Mitchell, Hunt, & Schmitt, 1986; Rabinowitz, 1989; Luo et al., 2007).

These results suggest that older adults are less likely than younger adults to spontaneously initiate elaborative encoding strategies, but can typically execute them when provided sufficient external support. This pattern is thought to arise due to age-related decline in prefrontal function. For example, neuroimaging evidence indicates that older adults typically exhibit reduced recruitment of the inferior prefrontal cortex relative to younger adults under intentional encoding conditions (Grady et al., 1995; Logan et al., 2002), suggesting reductions in spontaneous semantic elaboration and phonological rehearsal (Blumenfeld & Ranganath, 2007). However, when provided with a semantic orienting task to aid stimulus elaboration, older adults can recruit this region to a similar extent as younger adults (Logan et al., 2002), consistent with mitigation of age-related declines in spontaneous elaboration through the provision of a supportive encoding strategy. However, successful engagement of these strategies by older adults is often associated with bilateral recruitment of the prefrontal cortex, compared with asymmetric lateralized recruitment in younger adults (Cabeza, 2002;

Morcom, Good, Frackowiak, & Rugg, 2003), perhaps reflecting the compensatory need to recruit a more extended network of neural resources than younger adults to support elaborative encoding strategies.

Age Differences in Memory for Associations

Although the previous section described evidence demonstrating that age differences can be minimised in the context of recognition tests relative to free recall conditions, the same is not true when testing memory for associations. Indeed, one of the most commonly reported age-related changes in memory performance is a disproportionate decline in memory for associations, relative to memory for the individual items that comprise them (see Old & Naveh-Benjamin, 2008 for review). This is true for both within-domain associations, such as word pairs and picture pairs (Naveh-Benjamin, 2000; Cohn, Emrich, & Moscovitch, 2008; Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003), as well as between-domain associations, such as word-picture pairs (e.g., Naveh-Benjamin, Guez, Kilb, & Reedy, 2004). Notably, age differences in associative recognition performance are not typically driven by a decline in the ability to endorse studied pairs (e.g., hits), but rather by an increased rate of false alarms to recombined pairs, which are comprised of two studied items that were not originally paired together (e.g., Castel & Craik, 2003; Healy, Light, & Chung, 2005; Cohn et al., 2008). This does not reflect a generalized increase in responding ‘old’, but is specifically related to recombined pairs; when unstudied pairs comprise at least one novel element that was not encountered during the study phase, age-related increases in false recognition are typically no longer as evident (e.g., Naveh-Benjamin, 2000; Cohn et al., 2008).

This specific pattern of impairment suggests that age differences might arise due to problems at retrieval. In particular, an age invariant hit rate and false alarm rate to novel pairs, coupled with an increase in false alarms to recombined pairs, is suggestive of an age-related decrease in recollection, coupled with an increased reliance on familiarity (Cohn et al., 2008). That is, when a test pair includes a novel element that is not familiar, one can use the absence of familiarity to reject that pair. Similarly, when facing intact pairs, in which both elements have been studied, a reliance on familiarity will produce a correct response. In contrast, recombined pairs place significant demands on using recollection of original associates to overcome the familiarity of the individual elements comprising recombined pairs. The need to oppose familiarity with recollection of specific event details, or ‘recall-to-reject’, is described as a *disqualifying* strategy, as it involves targeting, retrieving, and evaluating specific details associated with past events in order to disqualify a familiar event as having occurred previously (Gallo, 2004).

The proposal that aging is associated with declines in recollection-based retrieval processes, coupled with an increased reliance on familiarity, is supported by evidence from other paradigms that similarly place recollection and familiarity in opposition. One task that has been designed to investigate this process is an exclusion task (Jacoby, 1991; Jacoby et al., 1993). In this paradigm, participants study items in one of two contexts, and then complete two tests that each target items that have been studied in one context but not the other. In order to reject studied lures from the alternative context, one must recall the context of each studied item before accepting it by successfully implementing a ‘recall-to-reject’ strategy. In contrast, accepting studied items and rejecting novel lures can be more easily supported by the presence or absence of familiarity. As in the associative recognition test, older adults tend to exhibit an intact hit rate, coupled with an increased false alarm rate to studied, but not non-studied, lures in exclusion tasks (Jennings & Jacoby, 1993; Gallo, Bell, Beier, &

Schacter, 2006; Gallo, Cotel, Moore & Schacter, 2007). This pattern provides further evidence for a specific decline in the ability to execute a ‘recall-to-reject’ strategy, coupled with intact, and perhaps an over-reliance on, familiarity-based retrieval.

Consistent with this idea, age differences in the recruitment of the prefrontal cortex, which has been linked with the execution of this strategy (Gallo, Kensinger, & Schacter, 2006; Gallo, McDonough, & Scimeca, 2010; Bowman & Dennis, 2016), have been observed in fMRI studies of associative memory and exclusion tests. For example, whereas younger adults exhibit increased activity in the prefrontal cortex during retrieval of associations relative to individual items, older adults do not display the same task-dependent increase (Giovanello & Schacter, 2011). Similarly, whereas younger adults exhibit increases in recruitment of the prefrontal cortex during an exclusion task when demands on ‘recall-to-reject’ processes increase, older adults exhibit persistent elevations in prefrontal activity during both low and high demand conditions (McDonough, Wong, & Gallo, 2013). Both of these patterns suggest that older adults may fail to adopt different retrieval strategies in response to changing task demands. In particular, older adults may fail to engage a recollection-based retrieval strategy when retrieving associations relative to individual items, instead relying on familiarity-based retrieval across conditions.

Although this evidence suggests that age differences during retrieval contribute to declines in associative memory, another factor that could give rise to this deficit is impairments during the initial encoding of the event. In particular, the ability to successfully execute a ‘recall-to-reject’ strategy requires the existence of a strong and specific association between items (Cohn et al., 2008). Evidence for age-related declines in the quality of initial encoding comes from observations that age differences in associative memory can be substantially reduced when the formation of associations is facilitated by either schematic or strategic support. For example, when two words are semantically related, thereby reducing demands on forming a novel link between the items, age differences in associative memory are minimised (Naveh-Benjamin et al., 2003). Similarly, the provision of encoding strategies that facilitate the formation of a strong link between items, such as sentence generation or visual imagery, also reduces the magnitude of age differences in associative memory (Naveh-Benjamin, Keshet Brav, & Levy, 2007). Such evidence is consistent with the idea that older adults typically fail to create robust representations of specific associations between unrelated items in the absence of schematic or strategic support. However, there is presently mixed evidence as to the source of this impairment.

On the one hand, it has been proposed that aging reduces one's ability to form novel associations between individual elements or attributes that comprise an event. According to this view, formalised as the *Associative Deficit Hypothesis* (Naveh-Benjamin, 2000), individual elements of an episode can be encoded into memory, but they are not successfully bound together to create a coherent event representation (Chalfonte & Johnson, 1996; Mitchell, Johnson, Raye, & D'Esposito, 2000; Naveh-Benjamin, 2000). This proposal is consistent with numerous examples of disproportionate deficits in associative memory relative to item memory among older adults, including impaired memory for associations between items and the contextual and perceptual details associated with an item's initial presentation (see Spencer & Raz, 1995 for review), coupled with intact memory for the item itself. For example, older adults are impaired in memory for which of two speakers read a word aloud, or in which of two modalities it was presented (McIntyre & Craik, 1987; Hashtroudi, Johnson, & Chrosniak, 1989), as well as spatio-temporal details associated with an item's presentation (Chalfonte & Johnson, 1996; Kausler, Lichty, & Davis, 1985;

Kausler & Wiley, 1990). Taken together, these age differences are thought to arise due to a common deficit in the ability to form novel associations, due to both declines in binding processes, as well as declines in the strategic processes necessary to create more robust associations.

Alternatively, it has been proposed that age-related decline in memory for associations arises due to the tendency to form too many associations, rather than too few. This idea, referred to as the *Hyper-Binding Hypothesis* (Campbell, Hasher, & Thomas, 2010), suggests that age-related declines in the ability to ignore irrelevant information (Hasher, Zacks, & May, 1989; Kim, Hasher, & Zacks, 2007), and delete previously relevant information from working memory (Hartman & Hasher, 1991; Hasher, Quig, & May, 1997), increases the likelihood that co-occurring and temporally contiguous information will become bound to target information. Such extraneous binding is predicted to lead to competition between relevant and irrelevant information during retrieval, resulting in impaired memory for target associations (e.g., fan effect: Anderson, 1983; Campbell et al., 2010). Evidence for this hypothesis comes from observations that older adults tacitly form associations between targets and co-occurring distractors in the environment, resulting in increased access to these associations in subsequent tasks (Campbell et al., 2010; Weeks, Biss, Murphy, & Hasher, 2016). Further evidence for this idea comes from observations that older adults are more likely to make false alarms to recombined pairs consisting of items that were originally presented close together in the study list, relative to those that were originally presented further apart (Campbell, Trelle, & Hasher, 2014). These results suggest that, in addition to increased reliance on familiarity during retrieval, older adults may also be more likely to make false alarms during associative recognition due to increased interference at retrieval that arises due to hyper-binding.

Neuroimaging evidence has identified age differences in neural activity during encoding that are consistent with age-related declines in encoding quality. For example, older adults typically exhibit reduction in both hippocampal and prefrontal activity during encoding of associations relative to younger adults (Cabeza et al., 1997; Mitchell et al., 2000). In particular, whereas younger adults exhibit increases in both prefrontal and hippocampal activity during associative encoding relative to item encoding, older adults fail to exhibit the same increase, resulting in disproportionate age differences in activity during encoding of associations relative to items (Dennis et al., 2008). Reduced hippocampal activity during associative encoding relative to item encoding is consistent with failure to adequately recruit this region to form novel associations between items (Chalfonte & Johnson, 1996), as suggested by the associative deficit hypothesis. However, reductions in prefrontal activity suggest a reduced tendency for older adults to engage attentional control mechanisms and elaborative encoding strategies to facilitate the formation of specific associations (Moscovitch, 1992; Craik & Rose, 2012), consistent with an inhibitory control deficit. Thus, existing work provides mixed evidence for these views, but together suggests that age differences in associative memory do arise, at least in part, due to age-related declines during encoding.

Age Differences in Mnemonic Discrimination

The previous sections describe pronounced age differences in memory for associations relative to single items, and for recall as compared to recognition. However, there are also conditions under which older adults exhibit dramatic impairments in recognition memory for individual items. Such age differences arise in recognition tests wherein participants are required to discriminate between stimuli that are highly similar. One experimental paradigm that exemplifies such conditions is an object recognition memory test that includes not only studied objects and novel foils, but also perceptually similar foils. In this type of paradigm, older adults are not typically impaired in endorsing studied pictures (e.g., hits) or rejecting novel foils (e.g., correct rejections), but often exhibit significant increases in the likelihood of incorrectly endorsing similar foils as studied (e.g. false alarms; Koutstaal, 2003; Kensinger & Schacter, 2008; Toner, Pirogovsky, Kirwan, & Gilbert, 2009; Holden, Toner, Pirogovsky, Kirwan, & Gilbert, 2013). Moreover, studies manipulating target-foil similarity have observed that age-related increases in false recognition tend to be absent or minimised at low levels of similarity, but rise as target-foil similarity increases (Stark, Yassa, Lacy, & Stark, 2013; Reagh et al., 2014). Put another way, a greater change in input (e.g., greater dissimilarity) is necessary for older adults to correctly identify lures as novel.

This observation has led to the proposal that aging is associated with an increased threshold for pattern separation (Toner et al., 2009; Stark et al., 2013; Reagh et al., 2014), which describes the ability for the hippocampus to assign distinct, non-overlapping representations to similar inputs (Norman & O'Reilly, 2003). This increased threshold for pattern separation is thought to result in an age-related shift towards pattern completion, the process by which stored representations are retrieved based on partial or degraded input (Norman & O'Reilly, 2003), resulting in false recognition of similar foils. Age-related changes in pattern separation and pattern completion are thought to arise due to declines in hippocampal function with age, in particular the dentate gyrus and CA3 subregions, which are thought to be critical for pattern separation and pattern completion, respectively (Yassa & Stark, 2011). In support of this idea, age-related increases in lure false recognition have been linked to increased activity in DG/CA3 subregions in older adults (Yassa et al., 2011; Yassa, Mattfeld, Stark & Stark, 2011), elevated firing rates in CA3 neurons in aged rodents (Wilson et al., 2005), and reductions in perforant path integrity in older adult humans (Yassa et al., 2010).

Despite evidence that pattern separation processes are involved in mnemonic discrimination (Bakker, Kirwan, Miller, & Stark, 2008), studies in younger adults have also linked successful performance with the use of a 'recall-to-reject' strategy, which involves retrieval of the original target representation in order to reject similar lures (Migo et al., 2009; Moliter, Ko, Hussey, & Ally, 2014). Critically, such a process requires pattern completion (Norman & O'Reilly, 2003), suggesting that false alarms and correct rejections may reflect both pattern separation and pattern completion processes to some degree, and that age-related increases in false recognition may result from impairments in both of these processes. As aging is associated with declines in the ability to execute a 'recall-to-reject' strategy, as described in the previous section (Jennings & Jacoby, 1993; Gallo et al., 2006; Cohn et al., 2008), this deficit may also contribute to age-related increases in false recognition. Importantly, the ability to use a 'recall-to-reject' strategy to avoid false recognition is thought to be partly determined by the degree to which stimulus details have been encoded successfully. For example, an eye-tracking study in younger adults found that lures subsequently rejected correctly were associated with a greater number of fixations during encoding as compared to lures that were falsely recognised (Moliter et al., 2014). Such findings raise the possibility that age-related increases in false recognition may arise due to impoverished stimulus encoding, thus reducing the availability of the detailed information needed to disqualify lures as having been studied.

On the one hand, it may be the case that older adults are more likely to encode general conceptual information than item-specific perceptual detail, and therefore experience reduced availability of these details during retrieval and increased reliance on semantic gist (Schacter, Koutstaal, & Norman, 1997). Evidence for this idea comes from observations that older adults are more likely to incorrectly judge non-studied objects as old when they belong to the same category as studied objects (Koutstaal & Schacter, 1997; Koutstaal, Schacter, Galluccio, & Stofer, 1999). Similarly, older adults are more likely than younger adults to misrecollect having studied semantic associates of recently presented word lists, erroneously recalling and recognizing words such as 'sleep' when 'doze' and 'bed' have been studied (Norman & Schacter, 1997; Tun, Wingfield, Rosen, & Blanchard, 1998; Kensinger & Schacter, 1999). Both of these effects suggest a reduction in the availability of item-specific details, coupled with increased reliance on general, conceptual information with age. In support of this idea, fMRI studies have observed age-related reductions in the recruitment of perceptual processing regions (e.g., fusiform cortex, extrastriate cortex) during encoding of visual stimuli, coupled with increased activity in lateral prefrontal regions that have been associated with encoding of conceptual, rather than perceptual, information (Grady, McIntosh, & Craik, 2003; Gutchess et al., 2005; Dennis et al., 2008). These findings are consistent with preferential encoding of general conceptual information, relative to perceptual detail with age.

However, it is also possible that age-related increases in false recognition of similar lures arise not only due to shared conceptual information between exemplars, but also due to overlapping perceptual features. Targets and foils in object recognition memory tests often share both perceptual and conceptual information, either of which may give rise to false recognition. Indeed, age-related increases in false recognition have been observed in the context of abstract objects that share perceptual features, suggesting that conceptual overlap is not essential to give rise to age-related deficits in performance (Pidgeon & Morcom, 2014). A role of perceptual similarity in false recognition among older adults is also consistent with previous work identifying that false alarm rate increases as perceptual similarity between exemplars increases, and does so more rapidly with age (Stark et al., 2013; Pidgeon & Morcom, 2014). The possibility that the age-related increase in false alarms to similar lures is driven by false recognition of perceptual features shared between exemplars is consistent with declines in representational quality with age.

In particular, it has been proposed that aging reduces the availability of unique, object-level representations that are necessary to disambiguate targets and foils with overlapping features, but leaves simpler, feature-level representations intact (Burke et al., 2010; 2011). Accordingly, novel objects that share overlapping features with studied objects appear familiar, leading to increases in false recognition. This idea is consistent with observations that age-related impairments in mnemonic discrimination emerge when interference at the feature level must be resolved by representations at the object level (e.g., targets and foils share feature overlap), but not when simple features can support successful discriminations (e.g., targets and foils are distinct). Such deficits may arise due to age-related declines in the function of the perirhinal cortex (Burke et al., 2014), which plays a critical role in supporting conjunctive, object-level representations (Cowell, Bussey, & Saksida, 2006). Consistent with this proposal, age-related reductions in the engagement of the perirhinal cortex during complex object discrimination tasks have been linked to impaired performance (Ryan et al., 2012). Thus, declines in representational quality may also play a role in age-related increases in false recognition of similar lures.

A Common Mechanism?

The previous sections have summarised three prominent examples of age-related memory decline that have emerged from research involving laboratory-based tests of episodic memory: i) impaired recall of event details in the absence of external cues, ii) disproportionate deficits in memory for associations relative to individual items, and iii) reductions in the ability to discriminate between similar events. Although each of these impairments has been identified in the context of very distinct experimental paradigms that seem to share little in common (e.g., memory for single items versus associations versus specific item details), there nevertheless appears to be a substantial amount of overlap in the nature of these deficits.

First, each case requires the formation of a complex event representation that contains specific, rather than general, encoding of the elements that comprise it. For example, remembering that you studied a word related to transport, rather than memory for the specific word *train,* will be insufficient to support recall of that target word. Similarly, remembering the words *apple* and *chair* were studied is not sufficient to support memory for whether they were originally paired together. Finally, remembering that an *umbrella* photo was studied is insufficient to discriminate between the studied umbrella and a perceptually similar umbrella at test that differs in its pattern or the shape of the handle. In each of these examples, subsequent memory is compromised when the event representation does not possess a sufficient level of complexity such that it uniquely specifies the event, rendering it vulnerable to interference from similar events. In support of this idea, enhancing the quality of initial event representations can often improve older adults' ability to recall information in the absence of retrieval support, remember associations, and discriminate between similar events. Taken together, this evidence suggests that memory impairments arise, at least in part, due to reductions in the quality of event representations with age.

The second element that is shared in common across each of these examples is that they place significant demands on the controlled retrieval of specific details of past events, and cannot be accomplished by relying on more automatic familiarity-based retrieval of general event details. For example, recalling details of previous experiences in the absence of any external cues necessitates the coordination of multiple controlled processes to execute a targeted search, reactivation, and evaluation of stored details. Similarly, retrieving associations entails overcoming familiarity of each of the elements comprising recombined pairs by recalling their original associates. Finally, specific details of studied objects must be recalled to overcome the familiarity of lures in a mnemonic discrimination task. Evidence from each of these paradigms reliably demonstrates substantial age-related deficits in engaging these controlled retrieval processes, coupled with increased reliance on more automatic processes. In support of this proposal, age differences in performance across each of these paradigms are reduced when demands on controlled retrieval processes are minimised. That is, in the context of item recognition, associative recognition, and object recognition with similar lures, older adults are not typically impaired at accepting old items, ostensibly because accurate memory in each of these conditions can be supported by more automatic, familiarity-based processes, even in the absence of the ability to recall specific details from the original encoding event.

Overall, the similarities in task demands associated with free recall, associative memory, and mnemonic discrimination suggest that age-related impairments across paradigms might be caused by two common factors: i) an age-related decline in the quality and complexity of event representations, and ii) an age-related reduction in the ability to engage in controlled retrieval and evaluation of event details. These deficits are consistent with declines with age in the structure and function of prefrontal and medial temporal lobe regions, which have been implicated in supporting these processes. Whereas the medial temporal lobes play a critical role in maintaining conjunctive representations that bind these details together into a coherent memory trace, the prefrontal cortex is critical for supporting the controlled and goal-directed processes required for elaboration and organisation of event details during encoding, and targeted search and evaluation processes during retrieval. Although the evidence reviewed thus far is consistent with age-related declines in both of these factors, this hypothesis remains to be explored systematically.

Thesis Overview

This thesis aims to further characterise the potential contribution of two factors that may be associated with age-related deficits in episodic memory: reductions in the quality of stimulus representations, and impairments in the execution of controlled and strategic retrieval processes. To assess the role of these factors, three experimental paradigms will be employed, each of which has been identified as highly sensitive to age-related deficits in performance, and which represent a varied sample of the laboratory-based tests of episodic memory that are often used to measure age-related changes in memory ability.

Chapter 2 investigates the efficacy of different encoding strategies for creating distinctive representations of common nouns by older adults, and the ability for these strategies to support memory performance both in the presence and absence of external cues (e.g., recall versus recognition). The results reveal that encoding strategies involving explicit elaboration that relies on prior semantic knowledge can enhance recall ability, but prominent age differences persist unless such strategies are combined with the provision of strong external cues. This experiment provides some evidence for contributions of both representational quality and strategic retrieval processes to age differences in recall of episodic memories.

Chapter 3 describes older and younger adults' ability to discriminate studied objects from highly similar lures under conditions that vary in the degree of retrieval support, as well as the level of interference from overlapping features. The results indicate that retrieval support alone is insufficient to mitigate age-related deficits in performance, whereas the combination of retrieval support and minimising interference yields substantial enhancements in older adults' performance. This Chapter additionally identifies relationships between recognition memory performance and individual differences in executive function, recall ability, and representational quality. The results of this chapter provide further evidence for separable contributions of representational quality and retrieval impairments to age-related declines in the ability to discriminate between similar events. Moreover, the neuropsychological data raise the possibility that that these declines may arise due to individual variability in brain function with age.

Chapter 4 uses pattern similarity analysis of fMRI data collected during an associative recognition task to characterise the neural mechanisms underlying age-related declines in representational quality and controlled retrieval processes that have been identified by the results of Chapters 2 and 3. This experiment finds evidence for declines in the differentiation of stimulus representations during encoding, as well as reductions in the ability to engage a 'recall-to-reject' strategy during retrieval, as indicated by the absence of event-specific reinstatement of encoding-related activity among older adults. Importantly, age-related declines in representational specificity are related to some, but not all, measures of retrieval-related reinstatement, suggesting that encoding quality contributes to age differences at retrieval, but that declines in controlled retrieval processes make additional, separable contributions.

Chapter 5 discusses the theoretical overlap between these different experimental paradigms, and describes a novel two-factor theory that may account for the full range of age-related deficits in episodic memory observed here. This proposal incorporates separable contributions of declines in representational quality and impairments in controlled retrieval processes that result from age-related changes in brain structure and function, and suggests that these factors may be well suited to explain the full range of episodic memory deficits experienced by older adults.

Chapter 2

Effects of controlled vs automatic elaborative encoding on recall and recognition

As described in Chapter 1, age differences in memory performance tend to be greatest when minimal environmental support is provided during encoding and retrieval in the form of orienting tasks that facilitate stimulus elaboration, and retrieval cues that minimise demands on controlled retrieval processes. Nevertheless, age differences in performance often persist even with the provision of this support. The experiment presented in this chapter will explore the possibility that residual age differences in performance arise due to persistent reductions in the quality of event representations among older adults, which fail to support successful retrieval, even when a high level of environmental support is provided in the form of a recognition test. To investigate this possibility, the present experiment explores multiple factors that might affect the efficacy of a given orienting task designed to support stimulus elaboration, both with respect to older adults' ability to execute them successfully, as well as their ability to enhance representational quality to a degree that can eliminate age differences in performance. Moreover, this experiment assesses whether improving representational quality alone is sufficient to eliminate age differences in memory performance, or whether additional factors, such as declines in controlled retrieval processes, also play a role.

Introduction

The critical influence of cognitive operations on stimulus representations and subsequent memory performance has been explored extensively in episodic memory research. These ideas form the basis of the depth of processing framework, which states that deeper levels of processing, such as evaluating a word based on its meaning, produce richer and more elaborate memory traces than processing of superficial characteristics, such as perceptual attributes, by facilitating more extensive stimulus differentiation and integration with existing knowledge (Craik & Tulving, 1975). The depth of processing framework was extended by Rogers and colleagues (1977) to include self-referential processing, with the observation that relating verbal stimuli to the self led to better retention than did semantic processing. This pattern, which has been replicated extensively using similar paradigms (see Symons & Johnson, 1997 for review), has led to the proposal that self-referential processing engages a unique form of stimulus elaboration that leads to the formation of richer and more differentiated memory traces than that produced by analogous stimulus processing in the semantic domain. These observations have generated a great deal of interest, particularly with respect to the potential application of self-referential processing as a mnemonic strategy in memory-impaired populations.

Of particular relevance in the present experiment is the recent proposal that self-referential processing may be particularly well suited to mitigating episodic memory impairment in older adults. These declines in episodic memory are driven in part by age-related deficits in initiating effective stimulus elaboration during encoding (Craik, 1983), which results in the formation of memory representations that lack specificity and are more prone to interference, giving rise to increases in memory errors (Koutstaal & Schacter, 1997). This encoding deficit is thought to arise due to declines in frontal lobe function and the availability of cognitive resources with age, which are critical for initiating elaborative encoding processes (Anderson, Craik, Naveh-Benjamin, 1998; Craik, 1983; Craik & Byrd, 1982; Moscovitch & Winocur 1995). Nevertheless, memory performance in older adults can be substantially improved when orienting tasks are provided at encoding to facilitate effective stimulus processing (Craik & Jennings, 1992; Zacks, Hasher, & Li, 2000). Accordingly, the discovery of encoding strategies that older adults can implement successfully in the face of concomitant declines in cognitive resources and frontally-mediated control mechanisms remains an important focus for ameliorating age-related impairments in episodic memory. However, the extent to which self-referential processing represents a unique form of stimulus elaboration that can serve as a particularly useful mnemonic device for older adults remains unclear.

Some studies have found that the self-reference effect remains intact with age, with older adults showing boosts to memory performance equivalent to those in younger adults following self-referencing relative to semantic processing (Glisky & Marquine, 2009; Hamami, Serbun, & Gutchess, 2011; Leshikar, Dulas, & Duarte, 2014; Rosa & Gutchess, 2013) or referencing a distant other (Gutchess, Kensinger, & Schacter, 2010; Gutchess, Kensinger, Yoon, & Schacter, 2007; Mueller, Wonderlich, & Dugan, 1986; Rosa & Gutchess, 2011; Yang, Truong, Fuss, & Bislimovic, 2012). Indeed, observations of an intact self-reference effect in older adults, as well as findings from divided attention studies in younger adults (Yang et al., 2012) have led to the suggestion that the mnemonic benefits of self-referencing occur relatively automatically and do not rely on controlled attentional processes. Such evidence suggests that self-referential processing might be particularly useful for older adults due to declines in frontal lobe function (Moscovitch & Winocur, 1995) and the availability of cognitive resources (Craik & Byrd, 1982). In contrast, some findings have indicated that the ability to benefit from self-referencing depends on executive function and resource availability (Gutchess et al., 2007; Turk et al., 2013), and is reduced in advanced old age (Glisky & Marquine, 2009) and therefore its potential utility for older adults may be limited. Finally, there is also evidence to suggest that self-referencing increases veridical recognition by enhancing fluency, and therefore also leads to age-related increases in false recognition, thus failing to produce a net improvement in memory performance (Rosa & Gutchess, 2013). These latter findings suggest that self-referencing may not prove to be an ideal strategy for older adults.

Critically, irrespective of the paradigm used or the specific pattern of results observed, none of the studies described above report a reduction or elimination of age- related differences in memory performance following the use of self-referential encoding strategies. This remains true even when age differences in retrieval processes are controlled for by providing a high level of environmental support at test, suggesting that differences in the quality of encoding give rise to the discrepancy in memory performance. One possible interpretation of these findings is that self-referencing is not an effective means of stimulus elaboration for older adults. However, an alterative explanation is that the simple orienting tasks (e.g., binary self-referential judgments, self-descriptiveness rating scales) that are typically used to assess the benefits of self-referencing are accompanied by additional, self-initiated elaboration in younger adults, which is not carried out spontaneously by older individuals (Rabinowitz, Craik, & Ackerman, 1982; Gutchess et al., 2007; Luo, Hendriks, & Craik, 2007; Treat & Reese, 1976), resulting in persistent age differences in memory performance. For instance, when deciding whether a trait is self-descriptive, younger adults may retrieve a memory of an occasion during which they exemplified that trait (Rogers et al., 1977), thus forming a richer stimulus representation, whereas older adults may recruit only the necessary abstract self-knowledge required to make the decision.

To investigate this possibility, the present experiment will explore the benefits of self-referential processing in older and younger adults using encoding strategies that inherently require participants to engage in more extensive stimulus elaboration, thereby better equating the nature and amount of stimulus differentiation performed across age groups. In particular, it compares traditional self-referential judgments to more elaborative self-referential encoding strategies that involve autobiographical memory retrieval, which can be divided into two sub-components. These include an episodic element that consists of specific memories from one's personal past tied to a spatio-temporal context, and a semantic element that consists of decontextualized knowledge about oneself and one's life experiences (Conway, 2005).

Importantly, a growing body of research indicates that these two forms of self-knowledge are functionally and anatomically distinct from one another. For instance, neuroimaging research has demonstrated that episodic and semantic autobiographical memory retrieval elicit separable patterns of neural activity (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Levine et al., 2004), and patients with neurological damage have been shown to exhibit intact self-knowledge coupled with impaired episodic retrieval (Grilli & Verfaellie, 2014; Klein, Loftus, & Burton, 1996; Tulving, Schacter, McLachlan, & Moscovitch, 1988), providing further evidence for a dissociation.

Consistent with the above evidence and most relevant to the current investigation is the stable finding that older adults exhibit declines in the specificity and richness of their autobiographical memories, coupled with intact and even preferential retrieval of personal and general semantic details (Levine et al., 2002). This pattern has been attributed to the additional demands that episodic memory retrieval places on selection, maintenance, and binding processes (Levine et al., 2004), which rely on the availability of attentional control and cognitive resources that decline with age (Craik, 1983; Craik & Byrd, 1972). Despite this distinction, no studies to date have compared the efficacy of episodic compared to semantic autobiographical elaboration on subsequent memory performance in older adults, nor how these encoding operations may improve retention beyond simple self-referential judgments.

Thus, the current investigation assessed memory for concrete nouns in older and younger adults following the use of self-referential and semantic orienting tasks that varied in response style, or the degree to which overt stimulus elaboration was inherently involved in making responses (see Figure 1). Specifically, traditional self-referential and semantic binary judgments were compared to three orienting tasks that involve more extensive stimulus elaboration through what will be termed 'narrative responses'. These included a semantic strategy (providing a definition of the target stimulus) and two self-referential strategies that varied in the component of autobiographical memory used for elaboration: an episodic autobiographical retrieval task that involved recalling a personal memory related to the stimulus, and a semantic autobiographical retrieval task that involved describing personal facts relating to the stimulus.

The efficacy of these encoding strategies was assessed by obtaining measures of memory performance at different levels of retrieval support, including free recall, cued recall, and recognition memory. This was motivated by the relative absence of research exploring the benefits of self-referencing on recall performance in older adults relative to younger adults (Bower & Gilligan, 1979; Klein, Loftus, & Burton, 1989; Warren, Chattin, Thompson, & Tomsky, 1983) and neurological patients (Grilli & Glisky, 2013; but see Mueller et al., 1986), despite age-related memory deficits being most pronounced under these conditions (Craik & McDowd, 1987). Thus, the present experiment extends previous findings by determining whether self-referencing can provided a mnemonic benefit to older adults in the absence of retrieval support, relative to analogous strategies in the semantic domain. The amount of explicit elaboration involved in performing the task at encoding, and the component of autobiographical memory used for elaboration, were both predicted to play an important role in determining this outcome.

Specifically, I predicted that more elaborative encoding strategies would provide substantial increases in memory performance relative to simple encoding judgments in both age groups, by virtue of their inherent access to a larger and more varied selection of stimulus attributes that should aid in the creation of a differentiated memory trace. However, due to age-related declines in the ability to self-initiate such processes, I expected older adults to exhibit larger benefits through the use of these strategies than younger adults, potentially mitigating age differences in memory performance relative to traditional encoding judgments. Among the encoding strategies in each response style, I predicted a self-reference benefit following traditional self-referential and semantic encoding judgments in both age groups, consistent with previous research. However, the pattern of performance expected with respect to the autobiographical and semantic narrative tasks was less clear.

In particular, previous research in younger adults suggests that episodic and semantic components of autobiographical memory provide equivalent mnemonic benefits, albeit through distinct mechanisms (Klein et al., 1989). Thus, it may be the case that performance in younger adults does not differ between these conditions. However, other research regarding episodic elaboration suggests that episodic self-referencing may provide some mnemonic benefits beyond that conferred by semantic self-knowledge. This is due to the additional complex cognitive operations involved in episode reconstruction and elaboration (e.g., scene construction, imagery, retrieval of perceptual and emotional details) and the creation of a unique and highly distinctive contextual cue to aid subsequent retrieval. However, if any additional benefit is observed in younger adults, it is less likely to extend to older adults. Consistent with previous research in memory-impaired patients described by Grilli & Glisky (2013), older adults may be limited in their ability to apply an encoding strategy that relies on episodic autobiographical retrieval, owing to the additional demands placed on executive control processes and cognitive resources that decline with age (Craik, 1983; Craik & Byrd, 1972).

In contrast, older adults should be able to use both personal semantic knowledge and general semantic knowledge just as effectively as younger adults to aid stimulus differentiation at encoding, as semantic retrieval remains intact with age (Nyberg, L., Backman, L., Erngrund, K., Olofsson, U., & Nilsson, L.G., 1996; Allen, P.A., Sliwinski, M., Bowie, T., & Madden, D.J., 2002; Levine et al., 2002). It is less clear how these two strategies will compare to one another. Although some previous research suggests that a self-reference benefit on memory should also emerge in such comparisons (Klein et al., 1989; Grilli & Glisky, 2013), few studies have compared two tasks that are matched with respect to the retrieval of a varied selection of stimulus attributes and differ only with respect to the involvement of the self. Thus, unless it is the case that self-referential processing provides a unique form of elaboration that cannot be achieved by semantic processing, I may find that elaborative semantic processing produces equivalent memory benefits as the retrieval of self-knowledge in both older and younger adults. Investigating this outcome in the present experiment will help to determine the utility of self-referential encoding strategies for enhancing recollection with age.

Method

Participants

Forty-eight younger adults (ages 18-30 years) and 48 older adults (ages 60-80 years) participated in the experiment. All participants were native English speakers. The younger adults were students from the University of Cambridge and the older adults were healthy, community-dwelling volunteers. Older and younger adults did not differ with respect to years of formal education ($t(94)=1.49$, $p > .10$, $d = 0.31$), and older adults scored higher than younger adults on the Vocabulary subtest of the Shipley Inventory of Living Scale, as is common in studies of cognitive aging (Shipley, 1986; $t(94)=8.36$, $p < .001$, $d = 1.72$). Twenty-four participants in each age group were randomly allocated to the episodic or semantic self-referencing condition. The demographic characteristics of these sub-groups are displayed in Table 1. The participants in each sub-group were matched for age, education, and vocabulary scores (all $p > .30$). The older participants were additionally tested using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), a brief screening tool for mild cognitive impairment, and performance on this measure did not differ between the episodic and semantic sub-groups ($t < 1$). All participants provided written informed consent prior to beginning the experiment using methods approved by the Cambridge Psychology Research Ethics Committee and received monetary compensation at a rate of £7.50 per hour for participation.

Table 1: Participant Demographic Information (means and SD)

	Younger Adults		Older Adults	
	Episodic Sub-Group	Semantic Sub-Group	Episodic Sub-Group	Semantic Sub-Group
N	24	24	24	24
Age	21.5 (2.57)	22.29 (2.79)	70.46 (6.06)	69.21 (4.85)
Gender	11M, 13F	10M, 14F	10M, 14F	6M, 18F
Years of Education	16.29 (1.33)	16.62 (1.74)	17.75 (2.38)	16.58 (3.30)
Shipley Vocabulary	33.42 (3.59)	33.42 (3.40)	37.92 (1.44)	37.96 (1.49)
Montreal Cognitive Assessment	-	-	27.13 (1.39)	27.58 (1.86)

Design

In the present experiment, I varied domain (self-referential, semantic) and response style (binary judgments, narrative responses) within-subjects in a factorial design to produce four different types of encoding strategies: a binary semantic task, a binary self-referential task, a narrative semantic task, and a narrative self-referential task (see Figure 1). Three out of the four orienting tasks were common to all participants, whereas the self-referential narrative response was varied between-subjects, with half of participants allocated to the episodic autobiographical sub-group and half of participants allocated to the semantic autobiographical sub-group. To summarise, the experiment design consisted of two within-subjects variables: domain (self-referential, semantic; within-subjects) and response style (binary judgment, narrative response; within-subjects) and two between-subjects variables: autobiographical condition (episodic, semantic) and age (younger, older).

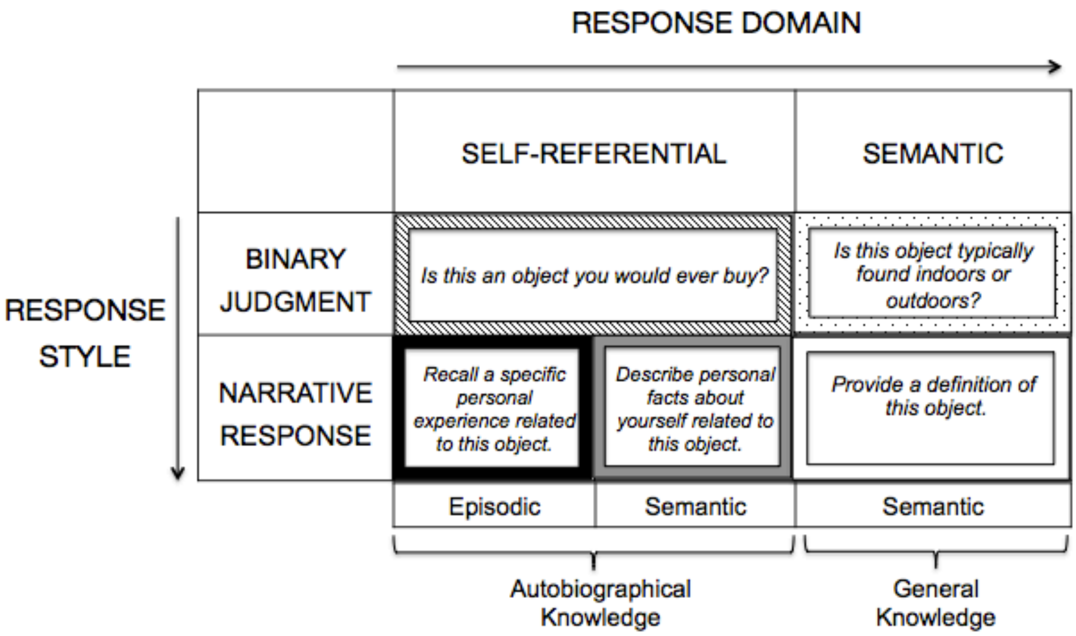

Figure 1. Experiment Design. During encoding, participants used four different orienting tasks, described in the figure above, to study a series of concrete nouns. Three out of the four orienting tasks were common to all participants, whereas the self-referential narrative response varied according to which subgroup participants were allocated: Those in the Episodic sub-group completed an autobiographical memory retrieval task, whereas those in the Semantic sub-group completed a task involving retrieval of conceptual knowledge about the self. The borders surrounding each orienting task correspond to pattern/colour of the bar depicting performance associated with that task in the graphs in Figures 2 and 3.

Materials

A total of 144 concrete nouns between 4 and 8 letters long were chosen from the Medical Research Council Psycholinguistic Database and used as stimuli. These words were divided into nine 16-item lists that served as stimuli in the study and test phases of the experiment. The lists were matched for concreteness, familiarity, imaginability, Kuceira-Francis frequency, and word length (all $F < 1$). Allocation of the lists to each condition during study and for use as foils in the test phase was counterbalanced across participants.

Procedure

The experiment consisted of six study-recall blocks followed by a recognition test at the end of the session. Three consecutive blocks consisted of self-referential responses, while the other three consecutive blocks consisted of semantic responses, with the order of the two sets of blocks counterbalanced across participants. A practice block preceded each three-block phase to ensure participants understood how to provide the appropriate self-referential and semantic responses.

Each of the six blocks began with a study phase wherein participants made responses to 16 words, 8 of which prompted binary judgments and 8 of which prompted narrative responses. The response type varied in an alternating fashion every two trials, with the name of the response to be performed located at the top of the screen and the word presented centrally. The self-referential binary judgment was termed the BUY response, and participants answered yes or no to the question, '*is this an item you would buy in the next year?*' The semantic binary judgment was termed the LOCATION response, and participants answered indoors or outdoors to the question, *'is this item typically found indoors or outdoors?*' The self-referential narrative response came in two forms; in the episodic autobiographical condition, participants provided a MEMORY response, and were asked to *recall and describe a specific episode from your past relating to the item,* whereas in the semantic autobiographical condition, participants provided a PERSONAL response, and were asked to *describe personal facts about yourself relating to the item.* The semantic narrative response was termed the DEFINITION response, and participants were asked to *provide a definition for this item.* Contrary to previous experiments using autobiographical retrieval or definition tasks (Grilli & Glisky, 2013; Klein et al., 1989; McDonough & Gallo, 2008), participants were required to give their narrative responses aloud so that I could be sure that they were performing the tasks correctly and with a sufficient level of detail. Furthermore, responding aloud enabled me to minimize the possibility of any response blending across tasks, or performing the incorrect task on a given trial, which is of particular concern in older adults who experience difficulties with task switching. Participants were provided with a maximum of 30 seconds to respond to each word and were encouraged to use all of the time they needed to perform the tasks effectively. This response window was motivated by previous research suggesting that response latencies for autobiographical retrieval can span up to 30 seconds (Conway, 2005), and enabled both older and younger participants to complete all narrative responses successfully.

The study phase was followed by a filled interval of counting backwards by threes for 30 seconds. This was immediately followed by a two-minute free recall period, in which participants were asked to write down as many words as they could remember from the preceding list. Next, participants were provided with the first two letters of each word from the study list in the order they were presented, with words that had already been successfully recalled filled in, and given a chance to recall any additional words from the list. After all six blocks were complete, participants completed a self-paced recognition test which consisted of all 96 studied words and 48 foils presented in random order. The vocabulary subtest of the Shipley Institute of Living Scale and the Montreal Cognitive Assessment (older adults only) were administered at the end of the experiment session.

Results

I first assessed how memory performance was affected by response style, domain, and age by conducting a 2 x 2 x 2 mixed analysis of variance (ANOVA) on performance in each sub-group with Age (younger, older) as a between-subjects factor and Domain (self, semantic) and Response Style (binary, narrative) as within-subject factors. This ANOVA was conducted in both the episodic and semantic autobiographical retrieval sub-groups, which differ only with respect to the nature of the self-referential narrative encoding strategy (see Figure 1 for a schematic of the experimental design). This analysis was performed on data from each level of retrieval support. However, as the cued recall performance paralleled that of free recall, only free recall and recognition data are presented below.

Recognition

Corrected recognition scores were calculated using the condition-specific hit rate, corrected by the pooled false alarm rate across conditions, and are depicted in Figure 2 and Table 2. The 2 x 2 x 2 mixed ANOVA revealed a Domain x Response Style interaction in both the episodic ($F(1,46) = 31.44$, $p < .001$, $\eta_p^2 = 0.406$) and semantic ($F(1,46) = 19.88$, $p < .001$, $\eta_p^2 = 0.302$) sub-groups. To explore this interaction, I conducted follow-up paired-sample t-tests comparing self-referential and semantic strategies in each response style (e.g., binary judgments, narrative tasks). This revealed a self-reference benefit following binary encoding judgments in both sub-groups (episodic: $t(46) = 2.95$, $p < .005$, $d = 0.87$); semantic: $t(46) = 4.11$, $p < .001$, $d = 1.21$), replicating previous findings of a self-reference effect in both older and younger adults. In contrast, the opposite effect was observed following narrative encoding strategies. Here, a benefit was observed of semantic processing in both the episodic ($t(46) = 3.44$, $p < .005$, $d = 1.01$) and semantic ($t(46) = 2.02$, $p < .05$, $d = 0.60$) sub-groups.

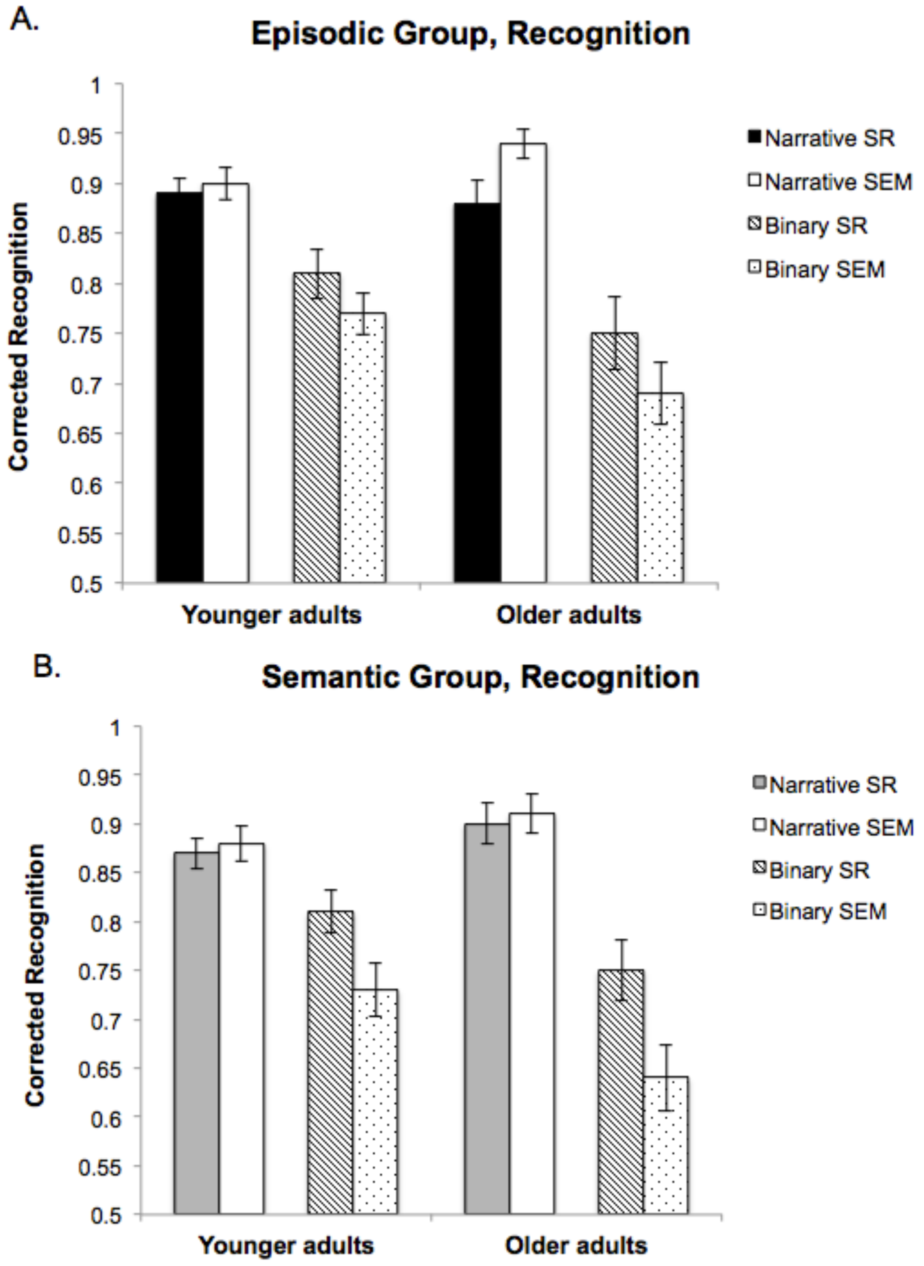

Figure 2. Recognition memory performance in the (A) Episodic Autobiographical condition and (B) Semantic Autobiographical condition across narrative and binary orienting tasks. In both conditions a self-reference benefit was observed on memory following the use of binary encoding judgments, but not narrative encoding responses. Additionally, an age-related deficit in memory performance was apparent following the binary encoding judgements, which was elimianted following the use of narrative encoding judgments.

The ANOVA additionally revealed a Response Style x Age interaction in both sub-groups (episodic: $F(1,46) = 7.37$, $p < .01$, $\eta_p^2 = 0.138$; semantic: $F(1,46) = 13.67$, $p < .005$, $\eta_p^2 = 0.229$). To explore this interaction, I conducted follow-up independent t-tests comparing recognition performance between age groups for words studied using binary judgments and narrative encoding strategies. These revealed persistent age-related deficits in performance following binary judgments (episodic: $t(46) = 1.83$, $p = .074$, $d = 0.54$; semantic: $t(46) = 2.26$, $p < .05$, $d = 0.67$), which were eliminated following the use of narrative encoding strategies in both sub-groups (all $p > .20$). These results indicate that older adults exhibited a larger benefit from the use of narrative encoding strategies relative to binary encoding judgments than did younger adults.

Free Recall

Participants' free recall scores reflect the proportion of total words correctly recalled from each condition across the three study blocks and are depicted in Figure 3 and Table 3. The 2 x 2 x 2 mixed ANOVA revealed a main effect of Age in both sub-groups (episodic: $F(1,46) = 74.24$, $p < .001$, $\eta_p^2 = 0.617$; semantic: $F(1,46) = 19.38$, $p < .001$, $\eta_p^2 = 0.296$), illustrating a significant age-related deficit in recall performance across encoding strategies. I also observed a main effect of Response Style (episodic: $F(1,46) = 94.38$, $p < .001$, $\eta_p^2 = 0.672$; semantic: $F(1,46) = 77.52$, $p < .001$, $\eta_p^2 = 0.628$), indicating a substantial benefit to recall performance in both age groups following the use of narrative encoding strategies relative to binary encoding judgments in both sub-groups. Furthermore, a Domain x Response Style x Age interaction emerged in the episodic sub-group ($F(1,46) = 4.67$, $p < .05$, $\eta_p^2 = 0.092$) but was not present in the semantic sub-group ($F < 1$).

To explore this interaction observed in the episodic sub-group, I conducted a 2 x 2 ANOVA with Age as a between-subjects variable and Domain as a within-subjects variable for each response style (e.g., binary, narrative). With respect to binary encoding judgments, I failed to detect a significant effect of Domain or a Domain x Age interaction (all $F < 1$). In contrast, the same ANOVA with respect to narrative encoding strategies revealed a main effect of Domain ($F(1,46) = 4.43$, $p < .05$, $\eta_p^2 = 0.088$) which was qualified by a Domain x Age interaction ($F(1,46) = 5.54$, $p < .05$, $\eta_p^2 = 0.107$). This interaction was driven by a self-reference benefit in younger adults that was absent from older adults, who recalled a similar number of words following episodic autobiographical elaboration and general semantic elaboration.

I next sought to determine whether recall performance following episodic autobiographical elaboration is indeed greater than recall performance following semantic autobiographical elaboration, and whether this is unique to younger adults. To address this question, I conducted a 2 x 2 ANOVA with Condition (episodic, semantic) and Age (younger, older) as between-subjects variables on free recall performance following the use of self-referential narrative strategies. This revealed an Age x Condition interaction ($F(1,3) = 5.51$, $p < .05$, $\eta_p^2 = 0.056$), confirming that episodic autobiographical elaboration supported superior recall to semantic autobiographical elaboration, and that this benefit was limited to younger adults.

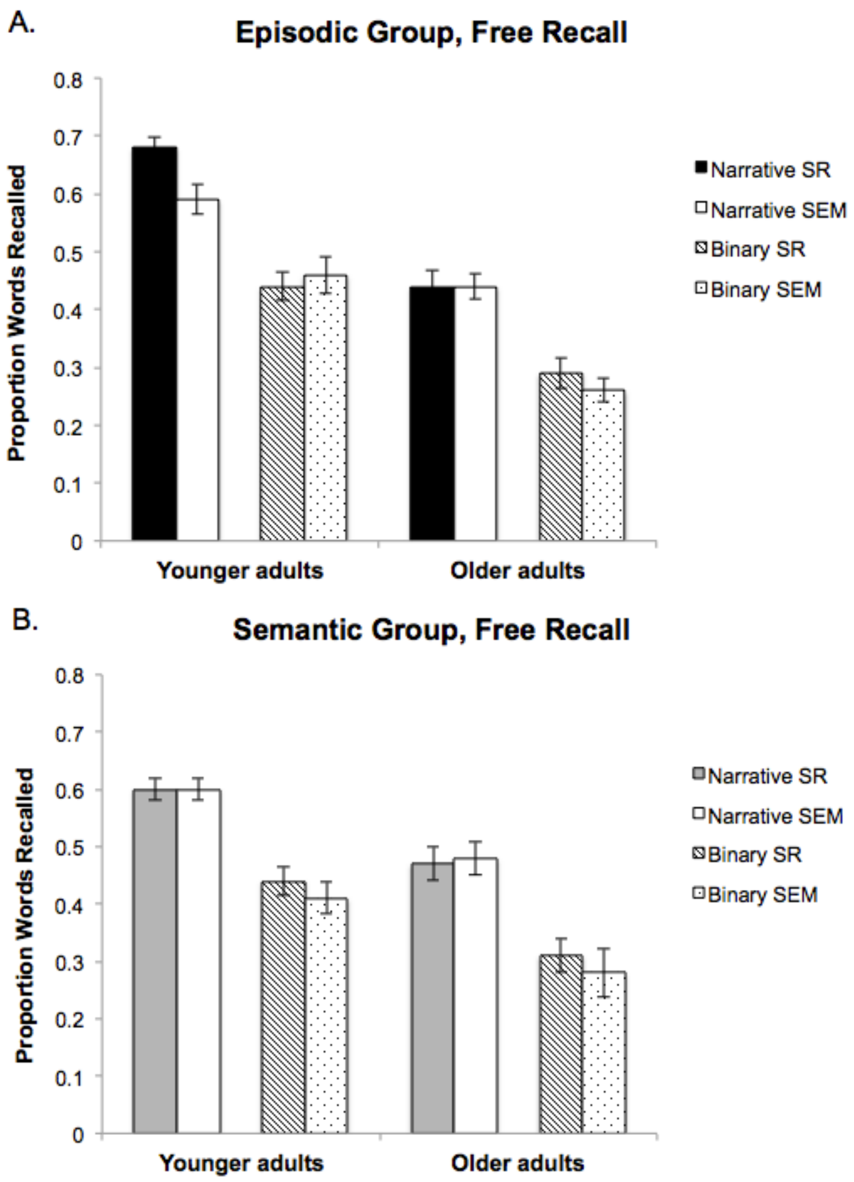

Figure 3. *Free recall performance in the (A) Episodic and (B) Semantic Autobiographical conditions across narrative and binary orienting tasks. In both conditions, older and younger adults recalled more words following narrative responses relative to binary judgments, and older adults recalled fewer words than did younger adults. In the Episodic Autobiographical condition (A), a self-reference benefit was observed following the narrative self-referential response in younger adults, but the same benefit was not observed in older adults. Neither age group exhibited a self-reference benefit following the binary judgments. In the Semantic Autobiographical condition (B), a self-reference benefit was not observed following the narrative responses or the binary judgments in either age group.*

Discussion

The present experiment sought to extend previous work exploring the self-reference effect in memory and further characterise its potential applicability as a mnemonic strategy to enhance recollection in older adults. To this end, I compared traditional self-referential and semantic encoding judgments that align closely with those used in past ageing research, to strategies that inherently provide more extensive stimulus elaboration through either retrieval of general semantic knowledge, or retrieval of episodic or semantic aspects of autobiographical memory.

With respect to self-referential and semantic binary encoding judgments, the present results replicate previous work demonstrating a self-reference benefit on recognition memory in younger and older adults (Glisky & Marquine, 2009; Hamami et al., 2011; Leshikar et al., 2014; Rosa & Gutchess, 2013), and extend them to memory for concrete nouns studied using a novel combination of self-referential and semantic orienting questions. However, the same pattern did not emerge during free recall, where memory performance was equivalent between the two conditions, suggesting that items encoded in relation to the self possessed greater potential memorability than those encoded using semantic judgments, but that this potential could not be realized in the absence of retrieval support. This may be due to the small proportion of 'yes' responses made to the self-referential encoding question, which made up less than half of total responses in both age groups. The high frequency of negative responses likely led to unsuccessful integration between words and the self-descriptive orienting question, which is thought to be more critical during free recall compared to recognition, when retrieval cues are absent from the environment and the encoding context becomes a vital internal cue for retrieval (Fisher & Craik, 1980).

Nevertheless, the observation that older and younger adults exhibited equivalent patterns of memory performance across both recognition and recall test conditions lends additional support to the proposition that the self-reference effect is intact with age. Furthermore, just as in previous work (Glisky & Marquine, 2009; Hamami et al., 2011; Leshikar et al., 2014; Rosa & Gutchess, 2013), older adults in the present experiment demonstrated significant impairments in recognition memory following the use of these strategies, as well as in recall performance. These results reinforce the idea that such simple orienting tasks perhaps rely too strongly on further, spontaneous elaboration by participants at encoding, or the initiation of more strategic and controlled retrieval processes to target a less distinctive memory trace. As such, simple encoding judgments do not appear to provide optimal encoding support for older adults, even when they involve self-referential processing.

Self-referencing in the context of narrative encoding strategies yielded a strikingly different pattern of performance, which differed between age groups. A comparison of episodic and semantic autobiographical retrieval revealed that younger adults recalled more words for which they had associated personal memories, a benefit that was not observed in older adults. Although previous work has indicated that these two forms of self-knowledge are functionally independent from one another (Grilli & Glisky, 2013; Klein, Loftus, & Burton, 1996; Klein et al., 1989; Levine et al., 2004; Tulving et al., 1988), the results from the present experiment suggest that retrieving different aspects of autobiographical memory during encoding elicits distinct mechanisms of stimulus elaboration that support varying levels of memory performance in healthy younger adults.

Interestingly, this benefit of episodic elaboration was specific to free recall; when words were provided as retrieval cues, this advantage was no longer evident.

This pattern suggests that the primary benefit of episodic relative to semantic autobiographical elaboration is the superior ability for specific events from memory to serve as effective internal cues for retrieval, relative to a series of personal facts about oneself related to the stimulus. This is consistent with previous research demonstrating that the uniqueness and ease of reconstruction of a cue is positively correlated with its ability to support retrieval of target information (Moscovitch & Craik, 1976), a benefit that has a greater influence on performance when external cues are not provided by the environment (e.g., free recall; Fisher & Craik, 1980). Although this benefit of episodic elaboration on free recall diverges from previous work comparing episodic and semantic forms of autobiographical elaboration (Klein et al., 1989; Grilli & Glisky, 2013), it is likely that methodological differences between experiments contributed to these differences. For example, previous studies that imposed stricter time constraints at encoding may have reduced participants' ability to reconstruct and elaborate a given episode, thus limiting the efficacy of this strategy.

In contrast to the pattern described above in younger adults, older adults did not demonstrate an additional enhancement to memory performance following episodic autobiographical elaboration, but exhibited equivalent recall of words that had been related to episodic and semantic components of the self. These results align with my predictions and are consistent with previous research demonstrating that aging is associated with a reduced ability to use specific contextual cues co-occurring in the encoding environment, a unique episodic memory in this case, to aid subsequent recall (Craik & Simon, 1980; Rabinowitz et al., 1982). This impairment has been attributed to declines in frontally mediated control processes and cognitive resources with age, which are essential for guiding the formation and retrieval of a strong, unique association between a study item and specific cue from the encoding context (Rabinowitz et al., 1982). In the present experiment, this deficit could have hindered the use of this strategy by older adults in a few different ways.

On the one hand, older adults may have been impaired in creating associations between episodic memories and stimulus words during encoding, an idea that is consistent with the associative deficit hypothesis of aging (Naveh-Benjamin, 2000). Alternatively, older adults may have created less specific associations during encoding, binding extraneous information that co-occurred in the encoding environment along with the target word, including other elements of the episode, or items that are semantically related to the episode concepts, a proposition consistent with the hyper-binding theory of aging (Campbell, Hasher, & Thomas, 2010; Campbell, Trelle, & Hasher, 2014). In either case, generation of a given memory at retrieval could have been less effective in uniquely targeting a list item, but rather led to high rates of intrusions of non-studied words by older adults.

An alternative possibility is that older adults retrieved event memories that were less specific and rich in episodic detail, thus lacking the distinctive contextual nature that characterized younger adults' responses. As a result, they might bear greater similarity to the responses provided during semantic autobiographical retrieval, resulting in equivalent performance. Although this is a plausible explanation of the results, detailed analysis of participant responses was not possible in the current experiment. Thus, the present results do not adjudicate between these possibilities, but identify a set of circumstances under which older adults are limited in their ability to apply self-referential encoding strategies in the same manner as younger adults. Future research should investigate whether a relationship exists between the quality of retrieved episodes and the efficacy of episodic encoding strategies in older adults, or whether this pattern is best explained by domain-general attentional control or binding deficits.

In contrast to the results described above, older adults were not impaired in their ability to implement encoding strategies that relied on the retrieval of personal or general knowledge from memory. This pattern is consistent with my predictions, and aligns with previous work indicating the retrieval of conceptual self-knowledge and general semantic knowledge remains intact with age (Allen et al., 2002; Levine et al., 2002; Nyberg et al., 1996). With the use of these narrative strategies, older adults exhibited memory performance at a level that was substantially greater than that achieved using binary encoding judgments. Moreover, during recognition this benefit was larger than that exhibited by younger adults, eliminating age differences in performance. This pattern lends support to the idea that previous evidence of persistent age-related deficits in recognition memory following traditional self referential and semantic encoding strategies emerged due to the spontaneous initiation of more extensive stimulus elaboration by younger adults, which was not carried out by the older group. Here, I observed that these age differences can be eliminated through the use of either self-referential or semantic strategies that inherently involve more extensive stimulus elaboration, combined with the provision of environmental support during retrieval.

Critically, the use of these narrative strategies not only enhanced recognition memory, but also free recall performance. This suggests that the increased number of stimulus attributes accessed in the service of these tasks facilitated the creation of distinctive and highly differentiated memory traces that were more accessible during retrieval. This was evident even in older adults, who typically exhibit deficits in self-initiated retrieval search and monitoring processes in the absence of external support

(Craik & McDowd, 1987; Dodson & Schacter, 2002). The amelioration of this deficit using the narrative encoding strategies in the present experiment indicates that older adults can also use cognitive operations to confer distinctiveness onto stimuli to aid recollection, a phenomenon that has only previously been observed in younger adults (Gallo et al., 2008; McDonough & Gallo, 2008). Although these tasks were also associated with significantly longer study durations than the binary judgments, response latencies during encoding were not correlated with performance across any of the narrative strategies, and it is unlikely that extended exposure to stimuli alone could explain the pattern of memory performance observed here. In particular, enhancement in recall performance suggests that the narrative encoding strategies did not simply increase stimulus familiarity, but supported the use of recollection-based retrieval processes such as the distinctiveness heuristic (Dodson & Schacter, 2002; Gallo et al., 2007).

Interestingly, I did not observe an advantage of self-referencing in my comparison of personal and general semantic encoding strategies in either age group. This pattern suggests that the memory benefits typically associated with self-referencing result from an increase in stimulus elaboration, or access to a greater number of stimulus attributes (e.g., general knowledge about the stimulus, as well as knowledge about the self in relation to the stimulus) relative to analogous semantic judgments, rather than a deeper or more meaningful form of stimulus elaboration uniquely associated with the self. As a result, when extensive elaboration is accomplished through access to a wide array of stimulus attributes in both semantic and self-referential orienting tasks, the degree to which one relates the stimulus to the self may be of little consequence to the quality of the resulting memory trace. In the present experiment, this pattern was observed even in the absence of retrieval support, which indicates that integration of the stimulus into the ‘self-schema’ is not necessary to provide useful cues for retrieval, as has been suggested previously (Rogers et al., 1977; Bower & Gilligan, 1979); integration with general knowledge works just as well. Thus, conceptual processing involving general and self-relevant knowledge may be thought of as alternative, yet comparably meaningful forms of elaboration for both younger and older adults.

It is important to note differences between the present experiment and previous research, which may have contributed to the results obtained here. In particular, I elected to use concrete nouns as opposed to trait adjectives as stimuli, adopting self-referential and semantic encoding judgments that that could be applied appropriately (Hamami et al., 2011; Hayama & Rugg, 2009). Although a previous meta-analysis of the self-reference effect in memory suggests that the effect is more variable when concrete nouns are used in place of trait adjectives (Symons & Johnson, 1997), numerous studies have observed a self-reference effect using non-trait adjective stimuli across a variety of different memory tests and populations (Bower & Gilligan, 1979; Grilli & Glisky, 2010, 2011; Hamami et al., 2011; Serbun, Shih, & Gutchess, 2011; Rosa & Gutchess, 2011; Warren et al., 1983). In light of these previous findings, as well as my replication of a self-reference benefit among contrasts that most resembled those conducted in previous research, it is unlikely that my choice of stimuli can explain selected instances where a self-reference benefit did not emerge in the current results. Nevertheless, future research should aim to replicate and extend the present findings using a range of stimuli to assess their generalizability to different experimental contexts.

Taken together, the present results indicate that the mnemonic value of self-referencing differs substantially depending on the nature of the orienting tasks used to investigate the effect. In particular, the involvement of the self per se appears to have a smaller impact on subsequent memory performance compared to other characteristics of the encoding strategy, including the degree to which extensive stimulus elaboration occurs spontaneously through implementation of a given task set, and whether the strategy involves the retrieval of episodic or conceptual details from memory. Thus, the data presented here are consistent with previous suggestions that the self is not a special mnemonic entity that operates via a specific, unitary mechanism (Gillian & Farah, 2005). Rather, I propose that the self simply represents a meaningful construct that can be applied flexibly to both contextual and conceptual encoding processes to aid stimulus differentiation and integration.

The observation that older adults can apply both self-referential and semantic encoding strategies that rely on existing knowledge just as well as younger adults, but are limited in their application of episodic self-referencing, indicates that the involvement of the self is neither necessary, nor sufficient, to enhance encoding operations in older adults. Thus, the present findings advance our understanding of appropriate encoding strategies for the elderly, which need not be self-referential in nature, but can similarly take advantage of the steady accumulation of general knowledge with age. Unfortunately, even the most effective encoding strategies in the present experiment did not eliminate recall deficits in the elderly group. This highlights the fact that age-related decline in episodic memory has a number of contributors, and enhancement of encoding operations can only go so far in diminishing this impairment. Thus, future research should focus on combining these strategies with those that can improve older adults' ability to initiate successful retrieval processes in the absence of environmental support to facilitate accurate recollection throughout the lifespan.

In summary, the results of this experiment suggest that age differences in recall performance could not be eliminated through the provision of encoding support alone, even when this came in the form of more elaborative encoding operations. Instead, providing external cues to support retrieval was also necessary to equate older adults' performance level to that of younger adults. These results are consistent with contributions of both declines in representational quality and impairments in controlled retrieval processes to age differences in memory performance. They additionally highlight the manner in which representational quality impacts demands on controlled retrieval processes, such that more distinctive event representations reduce demands on controlled retrieval, thus aiding recall and recognition in older adults. One limitation of the current paradigm is that, although the potential memorability of each word was clearly impacted by encoding operations, it is difficult to assess the resulting nature of event representations that supported word recognition in this paradigm. That is, even when performance was equated across groups, it may be the case that representational quality still differed between younger and older adults. This idea will be explored further in the next Chapter, which investigates this question using a mnemonic discrimination paradigm, thus better controlling the level of representational complexity required to support memory performance.

Chapter 3

Effects of interference and retrieval support on false recognition of similar lures

The results described in Chapter 2 lend support to the proposal that age-related decline in representational quality and controlled retrieval processes contribute to age differences in memory performance. The experiments presented in this Chapter explore this question further using a different paradigm that similarly places demands on both factors, but does so by asking participants to discriminate between studied objects and perceptually similar lures with varying levels of retrieval support. Accordingly, this investigation places more specific demands on the nature of the stimulus representation that must be available to support memory performance, thus further characterising how representational quality might change with age. By additionally varying levels of environmental support at retrieval, the experiments presented here aim to provide further insights into the degree to which age-related declines in mnemonic discrimination arise due to impairments in controlled retrieval processes, as compared to reduced availability of event details with age. Finally, this Chapter explores how individual differences in executive function, memory, and perception contribute to heterogeneity in memory performance among older adults.

Introduction

The episodic memory deficits observed in older adults are characterized not only by increased forgetting, but also greater susceptibility to false memories of events that did not occur (see Schacter, Koutstaal, & Norman, 1997 for review). Such memory errors are particularly evident when events are related to, or share overlapping elements with, those that were actually experienced (Koutstaal &

Schacter, 1997; Norman & Schacter, 1997; Kensinger & Schacter, 1999). One method of assessing vulnerability to false memories involves a recognition memory paradigm that requires individuals to discriminate between studied objects and novel ‘foil’ objects that are perceptually similar to those studied. In such paradigms, older adults are consistently more likely than younger adults to incorrectly identify similar foils as having been studied previously, even if there are no group differences in the ability to correctly identify previously studied targets as old (Koutstaal, 2003; Toner, Pirogovsky, Kirwan, & Gilbert, 2009; Yassa et al., 2011; Holden, Toner, Pirogovsky, Kirwan, & Gilbert, 2013; Stark, Stevenson, Wu, Rutledge, & Stark, 2015). Despite the frequent emergence and stability of this pattern among older adults, the underlying cause of this increase in false recognition remains unclear.

To gain insight into the source of this memory impairment, it is important to consider two distinguishing features of recognition memory tests that arise from the inclusion of similar foils. First, unlike a standard recognition memory test in which recollection and familiarity can both effectively support accurate memory judgments, the presence of similar foils significantly reduces the utility of familiarity (Migo et al., 2009; Norman, 2010). That is, when a target and its corresponding foil are perceptually similar and therefore both equivalently familiar, it can be difficult to set a criterion that can reliably distinguish targets from lures. Consequently, it becomes critical to use recollection of specific target details to overcome the sense of familiarity elicited by foils. The second key feature of a recognition memory test with similar foils is that memory for the conceptual or perceptual ‘gist’ of a stimulus is insufficient to support memory performance. As targets and foils share not only conceptual information but also significant overlap in perceptual features, accurate discrimination between targets and foils requires stimulus representations that contain a high degree of perceptual detail. Considering these features, age-related increases in false recognition could plausibly arise due to impaired recollection-based retrieval processes, declines in the quality of stimulus representations, or a contribution of both factors.

Age differences in strategic retrieval processes and in representational quality have been identified in previous research. For example, aging has often been associated with a disproportionate decline in recollection-based retrieval processes, leaving familiarity-based responding relatively intact (Yonelinas, 2002). In particular, age differences in performance are often greatest under conditions in which successful performance relies critically on the ability to recollect specific aspects of a stimulus or study episode in order to reject test probes that share similar or overlapping features. Age-related declines in the ability to engage these processes, often collectively referred to as a ‘recall-to-reject’ strategy, have been observed across a number of experimental paradigms (Jennings & Jacoby, 2002; Gallo, Bell, Bier, & Schacter, 2006; Cohn, Moscovitch, & Emrich, 2008; Luo & Craik, 2009). This impairment is thought to arise due to age-related declines in the ability to initiate controlled retrieval processes that are necessary to guide the reinstatement and evaluation of stored representations (Gallo et al., 2006; Gallo, Cotel, Moore & Schacter, 2007; Cohn et al., 2008; Luo & Craik, 2009). In support of this proposal, age differences in performance are often substantially reduced or eliminated when demands on strategic retrieval processes are minimized, such as when retrieval support is provided at test (e.g., recognition versus recall; Craik & McDowd, 1997), or when performance can be more readily supported by retrieval of distinctive attributes of prior events (Schacter, Israel, Racine, 1999; Gallo et al., 2007; Luo & Craik, 2009). Taken together, existing evidence suggests that declines in strategic retrieval processes, and in particular the ability to execute a ‘recall-to-reject’ strategy, may contribute to age-related increases in false recognition. However, this factor alone may not fully account for the increased propensity for older adults to incorrectly judge similar foils as having been studied previously.

In particular, age differences in the ability to discriminate between perceptually similar exemplars have been observed even when demands on controlled and strategic retrieval processes are minimized. For example, in paradigms using preferential viewing/exploration of novel objects, both aged humans and aged animals are more likely to treat novel objects as familiar (Burke et al., 2010; Yeung, Ryan, Cowell, & Barense, 2013). Similarly, in paradigms that should not incur any mnemonic demands, such as simultaneous perceptual discrimination tasks, age differences in target-foil discrimination have been identified in both humans and animals (Burke et al., 2011; Ryan et al., 2012; Newsome, Duarte, & Barense, 2012). Notably, these deficits are selectively observed when targets and foils share a high degree of perceptual overlap, and are absent when they can be distinguished on the basis of more simple features. This pattern suggests an increased reliance on representations of simple features and feature conjunctions that are shared by exemplars, perhaps due to a decline in the availability of complex, object-level representations that can resolve feature ambiguity between targets and similar foils (Cowell, Bussey, & Saksida, 2006). Accordingly, novel objects that are perceptually similar to studied objects appear familiar, leading to an increased incidence of false recognition (e.g., Burke et al., 2010; McTighe et al., 2010; Yeung et al., 2013).

To tease apart the potential contributions of declines in strategic retrieval processes and representational quality to age-related increases in false recognition of perceptually similar lures, test conditions can be compared that vary in their reliance on these factors. In the current investigation, I compare older and younger adults' performance on a standard Yes/No recognition test, wherein a single target or foil is presented on each trial, to a Forced Choice recognition test, wherein targets and corresponding foils are presented simultaneously. Although performance across these test formats can be similar when targets and foils do not share overlapping features (e.g., Khoe, Kroll, Yonelinas, Dobbins & Knight, 2000), a growing body of evidence suggests that distinct processes and neuroanatomical substrates can support performance on these two tests when targets and foils are perceptually similar. In particular, it has been proposed that the simultaneous presentation of targets and corresponding foils in forced choice tests enables judgments of relative familiarity between exemplars that can be supported by perirhinal cortex (PRC), whereas the item-wise presentation of targets and lures in yes/no tests requires the involvement of recollection-based retrieval processes that critically rely on the hippocampus (Norman, 2010).

In support of this proposal, previous work in younger adults has shown that instructions to rely on familiarity alone can support accurate performance in the Forced Choice format, whereas successful performance in the Yes/No format is determined predominantly by a participant's ability to use a 'recall-to-reject' strategy (Migo, Montaldi, Norman, Quamme, & Mayes, 2009). Further evidence for this dissociation comes from patient studies that observe selective deficits in Yes/No performance in individuals with focal hippocampal lesions (Holdstock et al., 2002a) and amnestic mild cognitive impairment (Westerberg et al., 2006; Westerberg et al., 2013). In contrast, individuals with more advanced Alzheimer's disease, affecting both the hippocampus and perirhinal cortex (PRC), exhibit impairments across both test formats (Westerberg et al., 2006; Westerberg et al., 2013). In the same patients, hippocampal volume was related to performance in both test formats, whereas PRC volume was selectively related to Forced Choice but not Yes/No performance (Westerberg et al., 2013). This observation is consistent with the role of PRC in familiarity-based judgments in object recognition (Brown & Xiang, 1998; Henson, Cansino, Herron, & Rugg, 2003), and also in its proposed role in supporting complex object-level representations that are critical for disambiguating targets and foils with overlapping features (Cowell et al., 2006; see Bussey & Saksida, 2007 for review).

Taken together, this evidence suggests that performance in a Yes/No recognition test with similar foils is determined primarily by one's ability to engage recollection-based retrieval processes. In contrast, though the availability of highly detailed perceptual representations is essential for performance across both test formats, this factor appears to have a more direct impact on performance in the Forced Choice test. This may arise from the significant reduction in strategic retrieval demands in this test format owing to the simultaneous presentation of targets and corresponding foils, resulting in closer correspondence between representational quality and recognition memory performance. Accordingly, a selective deficit in Yes/No performance in older adults would provide evidence for a role of impaired strategic retrieval processes, and suggest that perceptual representations of stimuli remain intact with age. Alternatively, impairments across both test formats would additionally implicate a decline in representational quality in age-related increases in false recognition.

To summarize, the present investigation compares older and younger adults' recognition memory performance across Yes/No and Forced Choice test formats to assess the degree to which declines in i) representational quality and ii) strategic retrieval processes contribute to age-related increases in false recognition of similar foils. Experiment 1 includes modified remember-know judgments to assess the degree to which participants recall specific stimulus details in order to endorse targets and reject lures. Experiment 2 assesses the effects of interference from intervening stimuli on the ability to discriminate between targets and foils in each test format. Finally, a follow-up neuropsychological assessment was conducted in a subset of older adults from Experiments 1 and 2 to assess how individual variability in representational quality, recall ability, and executive function might differentially relate to performance across test conditions.

Experiment 1

The aim of the first experiment was to investigate the degree to which age-related decline in object recognition memory performance could be ameliorated when demands on strategic retrieval processes are reduced through provision of environmental support at test. To this end, I compared older and younger adults' recognition memory performance across Yes/No and Forced Choice test formats. If age-related increases in false recognition are driven solely by impairments in strategic retrieval processes, I would predict that older adults should be impaired in the Yes/No test format, but exhibit intact performance in the Forced Choice format, where these demands are significantly reduced through the simultaneous presentation of targets and corresponding foils at test. In contrast, if declines in representational quality additionally contribute to age-related increases in false recognition, older adults should also exhibit impaired performance in the Forced Choice test due to reduced availability of complex, object-level representations that are capable of effectively disambiguating targets and foils with overlapping features.

I also included modified remember-know judgments at test in order to assess whether the contribution of recollection to false recognition decisions differs with age. Unlike the classic Remember-Know (RK) paradigm, wherein participants provide an indication of the subjective memory experience that accompanies ‘old’ responses, the modified procedure additionally asks participants to make this judgment regarding ‘new’ responses (Migo et al., 2009). Moreover, ‘remember’ responses here differ from those in the classic RK paradigm, in which retrieval of any qualitative information about the study event is associated with a ‘remember’ response (e.g., Koen & Yonelinas, 2010). Instead, ‘remember’ responses are defined in the present experiment as those events where the retrieval of specific perceptual details of the studied object is used to support recognition decisions. Accordingly, the frequency of ‘remember’ responses provides an indication as to how often participants are using a ‘recall-to-accept’ strategy to identify targets as old, and a ‘recall-to-reject’ strategy to disqualify lures as having been studied. It additionally allows me to determine whether false recognition decisions arise primarily due to increased familiarity-based responding in older adults, or due to misrecollection of stimulus details.

Method

Participants

Thirty-two younger adults aged 18 to 28 years ($M = 22.66$, $SD = 3.04$) and 32 older adults aged 60-80 years ($M = 70.47$, $SD = 4.59$) participated in the first experiment. All participants were native English speakers. The younger adults were students from the University of Cambridge and the older adults were healthy, community-dwelling volunteers. The groups were matched with respect to years of formal education ($t < 1$) and the older adults outperformed the younger adults on the vocabulary sub-test of the Shipley Inventory of Living Scale (Shipley, 1986; $t(62) = 3.47$, $p < .005$, $d = 0.881$). Older adults were additionally screened for cognitive impairment using the Montreal Cognitive Assessment (MoCA) and all participants performed within the normal range (*M* = 28.03, *SD* = 1.03). A summary of demographic information can be found in Table 1.

Table 1: Demographic information for participants from experiments 1 & 2

	Experiment 1		Experiment 2	
	Younger Adults	Older Adults	Younger Adults	Older Adults
N	32	32	34	45
Age	22.66 (3.0)	70.47 (4.6)	21.74 (2.4)	69.76 (5.6)
Education	16.72 (2.1)	17.81 (6.0)	16.08 (1.9)	16.47 (3.2)
Shipley	35.50 (2.3)	37.41 (2.1)	34.09 (3.2)	37.51 (2.1)
MoCA	--	28.03 (1.0)	--	28.11 (1.2)

Materials

A total of 800 color images of everyday objects were used as stimuli. This set consisted of 400 unique pairs of everyday object exemplars, collected from a combination of online sources, including Google Image Search (Mountain View, CA) and the stimulus sets available from the Konkle Lab (http://konklab.fas.harvard.edu). Each exemplar pair shared the same label (e.g., umbrella) and possessed a degree of feature overlap (e.g., shape, colour, pattern) such that targets and foils could not be discriminated without a detailed representation of each object (see Figure 1). To minimize any effects of pairwise variability in target-foil similarity on performance, an independent sample of participants rated exemplar pairs on perceptual similarity. I then created stimulus lists with equivalent levels of target-foil similarity on average, and counterbalanced the assignment of stimulus lists to test format and study block across participants.

Procedure

Each session began with a practice block in which participants completed an abbreviated version of the task that provided feedback on performance accuracy. Each participant then completed two study-test blocks, with the procedure identical for each block of the experiment. A short 5-minute break divided the first and second block during which participants performed the Shipley Institute of Living Scale. Older adults additionally completed the MoCA at the end of the testing session.

During each study phase, participants were presented with 200 pictures of everyday objects for 3000 ms each and instructed to judge the pleasantness of each object. After a 60 second filled interval during which participants counted backwards by sevens from a random 3-digit number, participants completed a recognition memory test. One half of the test comprised a forced choice format, wherein a target and foil were presented simultaneously, one on the left of the screen and one on the right. The other half of the test was in a Yes/No format, wherein a single exemplar was presented in the center of the screen, which could be either a target or a foil. Prior to the beginning of each test format, participants were reminded of the instructions and response options for that test. The order of the test formats was consistent across both blocks and counterbalanced across participants.

During each test phase, participants followed a modified remember/know procedure, indicating both their recognition decision and the nature of their memory for the object by selecting from four response options (see Figure 1). In the Forced Choice test, participants were instructed to select a ‘remember left’ or ‘remember right’ response if they could recall specific details of the exemplar they judged to have been previously studied, and a ‘familiar left’ or ‘familiar right’ response if their decision was based on greater relative familiarity of one exemplar over the other. In the Yes/No test, participants were instructed to select a ‘remember’ response if they recalled specific details of a studied exemplar and used these details to either accept a target (‘remember old’) or to reject a foil (‘remember new’). Participants were instructed to select a ‘familiar’ response if they were unable to recall specific details of a studied exemplar, and based their decision on the presence (‘familiar old’) or absence (‘unfamiliar new’) of familiarity for the presented object.

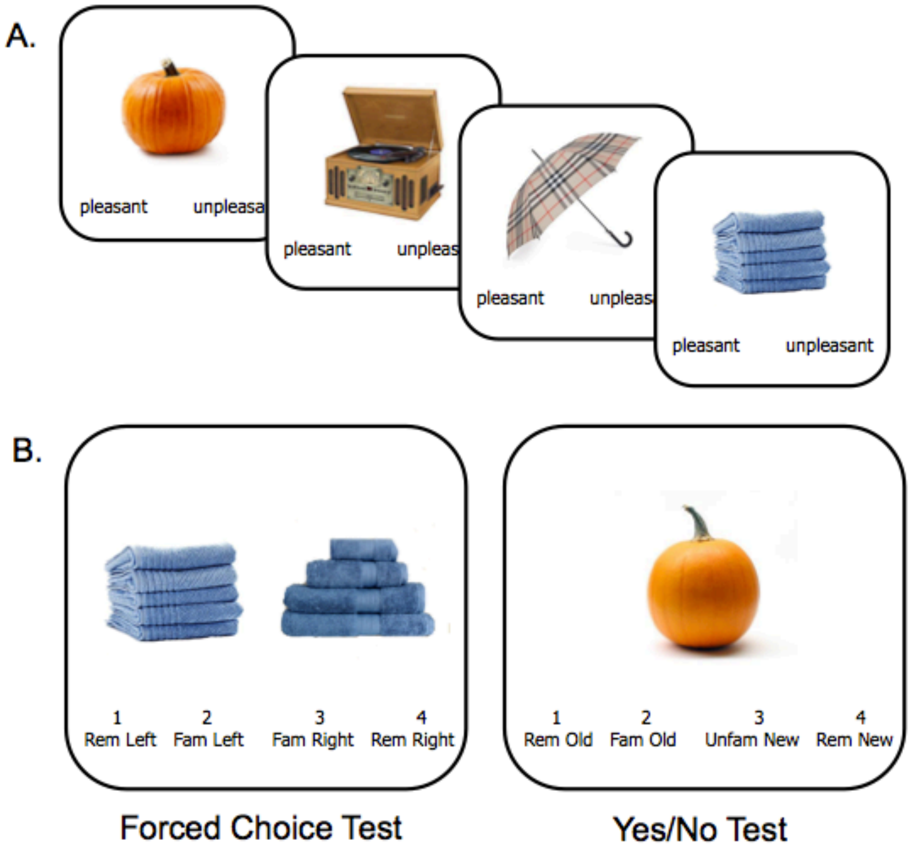

Figure 1: *A. Study phase schematic depicting example of experimental stimuli. B. Sample Forced Choice and Yes/No test trials. Response options refer to the modified ‘Remember/Know’ judgments in Experiment 1. In Experiment 2, participants made simple Left/Right and Old/New judgments for the Forced Choice and Yes/No tests, respectively.*

Results

I first compared recognition memory performance across age groups in the Forced Choice and Yes/No test formats, collapsing across remember and familiar responses (see Figure 2). This was done by computing *d*' scores from the proportion of correct responses in the forced choice test and the proportion of hits and false alarms in the Yes/No test (Macmillan & Creelman, 1991), and submitting these scores to a 2 x 2 mixed ANOVA with Test Format (FC, YN) as a within-subjects factor and Age (young, old) as a between-subjects factor. The ANOVA revealed that both older and younger adults performed significantly better on the Forced Choice test relative to the Yes/No test ($F(1, 62) = 45.61, p < .001, \eta_p^2 = 0.424$), and that older adults performed significantly worse than younger adults across both test formats ($F(1, 62) = 11.84, p < .005, \eta_p^2 = 0.160$), with the size of this deficit equivalent across test format ($F < 1$).

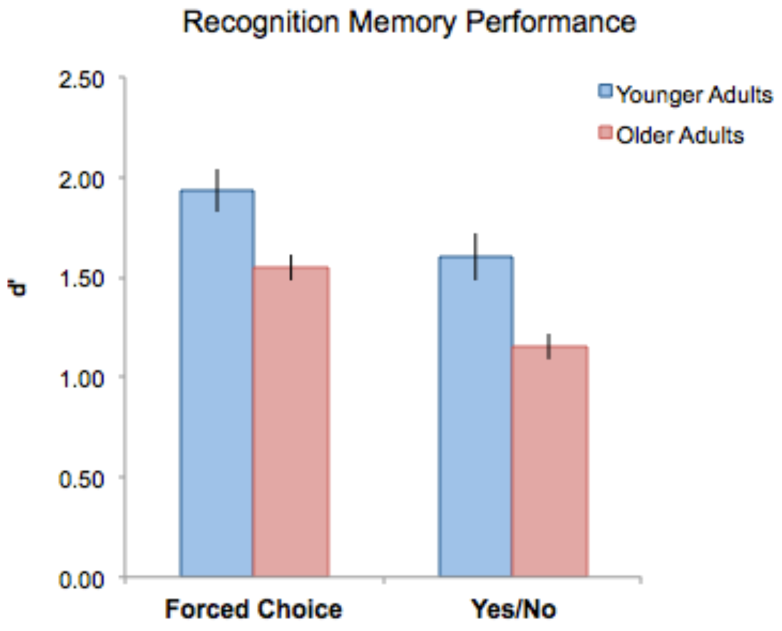

Figure 2: Recognition memory performance (d-prime) in the Forced Choice and Yes/No test formats from Experiment 1, collapsed across 'remember' and 'familiar' judgments. Age differences in performance were observed across both test formats.

Next, I explored the contribution of recollection to recognition decisions in older and younger adults. In the Forced Choice test, this meant assessing the proportion of ‘remember’ and ‘familiar’ responses to correct and incorrect decisions, whereas in the Yes/No test, this includes an assessment of the proportion of ‘remember’ and ‘familiar’ responses across all four response types, including hits, false alarms, misses, and correct rejections. Turning first to the Forced Choice test, no age differences emerged in the proportion of correct ‘remember’ responses to old items ($t < 1$), whereas older adults made significantly more incorrect ‘remember’ responses to similar lures ($t(62) = 2.59$, $p < 0.05$, $d = 0.657$). In contrast, no age differences were found in the proportion of correct or incorrect ‘familiar’ responses (*t*s < 1). A similar pattern was observed with respect to Yes/No recognition decisions. Again, no age differences were detected in the proportion of correct ‘remember’ responses to old items (e.g., hits; $t < 1$), whereas older adults exhibited a significant increase in the proportion of ‘remember’ false alarms to lures ($t(62) = 3.21$, $p < 0.005$, $d = 0.815$), accompanied by a reduction in the proportion of ‘remember’ correct rejections of lures ($t(62) = 3.23$, $p < 0.005$, $d = 0.820$). In contrast, no significant age differences emerged in the proportion of familiarity-based false alarms ($t(62) = 1.60$, $p = 0.114$, $d = 0.406$), nor in the proportion of ‘familiar’ hits, ‘unfamiliar’ correct rejections, or in ‘remember’ or ‘unfamiliar’ misses (*t*s < 1).

Discussion

In Experiment 1, older adults’ memory performance was assessed in a recognition memory test with similar foils using a standard Yes/No test format and a Forced Choice test format. If age-related increases in false recognition arise solely due to impairments in strategic retrieval processes, I predicted selective age differences in Yes/No performance, coupled with intact Forced Choice performance.

In contrast, if declines in representational quality also contribute to age-related increases in false recognition, I predicted memory deficits to emerge in both test formats. The results of Experiment 1 revealed age differences in both Yes/No and Forced Choice performance, indicating that impaired strategic retrieval processes alone cannot account for age differences in performance, and that age-related decline in representational quality is playing a role. In particular, age differences in Forced Choice performance are consistent with reduced availability of complex object-level representations, leading to an increased reliance on memory for simple features that are shared among targets and foils (Cowell et al., 2006). Such representations typically fail to support accurate discriminations between exemplars, even in the absence of explicit demands on controlled retrieval processes (Burke et al., 2010; 2011; Ryan et al., 2012; Yeung et al., 2013).

The results of the Remember/Know judgments suggest a reduction in the use of strategic retrieval processes with age, and are also consistent with the proposal that declines in the quality of stimulus representations contribute to this deficit. In particular, older adults exhibited a significant reduction in the proportion of 'remember-new' responses in the Yes/No test, which is consistent with a reduction in the use of a 'recall-to-reject' strategy (Migo et al., 2009). However, this was accompanied by an increased rate of incorrect 'remember' responses to lures, and this was true across both test formats. The presence of this deficit in the Forced Choice test is consistent with a decline in the availability of object representations that can disambiguate targets and lures. Moreover, although older adults did not exhibit a decline in the proportion of accurate 'remember' responses to studied items across test formats, the high rate of these responses to non-studied lures calls into question the degree to which older adults were indeed retrieving information that was unique to the studied stimulus to support these judgments. Instead, it is likely that 'remember' responses were more often accompanied by the retrieval of representations of features that participants believed were diagnostic of the studied stimulus, but that were actually shared by targets and foils due to the substantial overlap between exemplars.

Although this pattern of results suggests that declines in representational quality contribute to increases in false recognition with age, it remains unclear whether this single factor drives impairments across both test formats. For example, I cannot rule out the possibility that additional impairments in strategic retrieval processes also contribute to age differences in Yes/No performance. Therefore, in Experiment 2, the presence of interference was manipulated in efforts to control for age differences in representational quality, in order to assess whether these conditions can indeed ameliorate age differences in Forced Choice performance, and if so, whether age differences in Yes/No performance persist.

Experiment 2

Previous work indicates that reduced availability of complex, object-level representations is particularly detrimental to discrimination ability when feature overlap between targets and foils is high, and when interference from repeated lower level features is present (Cowell et al., 2006; Bartko et al., 2010; McTighe et al., 2010; Yeung et al., 2013). These conditions characterized the paradigm in Experiment 1, where there was not only a high degree of feature overlap between targets and foils, but also a buildup of feature level interference due to the use of long study lists containing a large number of objects sharing many lower-level features. If stimulus representations become compromised with age, leading to greater reliance on lower level representations, older adults would likely be more susceptible to feature-based interference across study trials, reducing their ability to accurately discriminate between targets and foils with overlapping features. Accordingly, age differences would be predicted to emerge in any task that requires conjunctive, object-level representations for successful target-foil discriminations, even when demands on controlled retrieval processes are minimised, as observed in the Forced Choice test in Experiment 1.

In Experiment 2, this possibility was explored by manipulating the number of stimuli presented in each study phase, in accordance with previous work indicating that longer study lists create a greater amount of interference from lower level features that are shared across items (Cowell et al., 2006). Specifically, I compared older and younger adults' performance in both test formats while varying the number of items in the study list across study-test cycles. The length of each study list was varied differently according to age group, such that the longer study list for older adults was the same length as the shorter list in younger adults. This enabled a comparison of memory performance across age groups when older adults faced an equivalent amount of interference relative to younger adults, as well as when they faced reduced interference relative to younger adults. If age differences in representational quality drive increases in false recognition across test formats, minimising interference should improve performance in both the Forced Choice and Yes/No test formats. In contrast, if age differences in strategic retrieval processes also contribute to age-related deficits in Yes/No recognition, minimizing interference should selectively improve performance in the Forced Choice test, where demands on these retrieval processes are significantly reduced.

Method

Participants

A new group of thirty-four younger adults aged 18 – 28 years (*M* = 21.74, *SD* = 2.39) and 48 older adults aged 60-80 years (*M* = 70.29, *SD* = 5.86) participated in this experiment. All participants were native English speakers. The younger adults were students from the University of Cambridge and the older adults were healthy, community-dwelling volunteers. Older and younger adults did not differ with respect to years of formal education ($t < 1$) and older adults scored significantly higher on the Vocabulary subtest of the Shipley Inventory of Living Scale ($t(77) = 5.77$, $p < 0.001$, $d = 1.315$). Three older adults were excluded from the analyses because they performed below the normal range (< 26) on the MoCA, leaving 45 healthy older adults who performed well within the normal range (*M* = 28.11, *SD* = 1.19). A summary of demographic information can be found in Table 1.

Materials

A total of 960 color images of everyday objects were used as stimuli. This set consisted of the 800 images used in Experiment 1, plus an additional 160 images obtained from similar sources to produce 480 unique pairs of object exemplars. These object pairs were divided into eight 60-item lists, with the allocation of each list to the short and long block length and to the Forced Choice and Yes/No test format counterbalanced across participants. As in Experiment 1, each exemplar in a pair served equally often as the studied target and unstudied foil.

Procedure

The procedure for this experiment was identical to that of Experiment 1, with the following exceptions. Participants completed two study-test blocks of unequal length, with length scaled for each age group based on the results of pilot experiments. Younger adults studied 180 items in their short block and 300 items in their long block, whereas older adults studied 60 items in their short block and 180 items in their long block. This resulted in a reference block of the same length completed by both groups, coupled with a block that was shorter or longer than the reference block for older and younger adults, respectively. The order of the short and long blocks was counterbalanced across participants. The test phase was again divided into a Forced Choice Test and a Yes/No Test, with test order consistent across blocks and counterbalanced across participants. Unlike Experiment 1, participants made simple Left/Right and Yes/No decisions in the Forced Choice and Yes/No formats, respectively, without the addition of modified Remember/Know judgments.

Results

As in Experiment 1, *d'* scores were computed to compare older and younger adults' recognition memory performance in the Forced Choice and Yes/No Tests at each block length (Macmillan & Creelman, 1991). Before exploring the effects of interference on performance, I first assessed performance when the two groups faced an equivalent amount of interference, namely for the reference block containing 180 stimuli, which is depicted in Figure 3a. To this end, I conducted a 2 x 2 mixed ANOVA with Test Format (FC, YN) as a within-subject factor and Age (young, old) as a between-subject factor. The results replicated those observed in Experiment 1, with i) both older and younger adults performing significantly better in the Forced Choice test relative to the Yes/No test ($F(1,77) = 15.15, p < 0.001, \eta_p^2 = 0.164$), ii) older adults performing significantly worse than younger adults across both test formats ($F(1,77) = 10.13, p < 0.005, \eta_p^2 = 0.116$), and iii) the size of this age effect being equivalent across test formats ($F < 1$).

I next examined the effects of increasing interference, that is, increasing block length from 60 items to 180 items in older adults and from 180 to 300 items in younger adults (see Figure 3b). To do so, participants' *d'* scores were submitted to a 2 x 2 x 2 mixed ANOVA with Block Length (short, long) and Test Format as within-subject factors and Age (young, old) as a between-subjects factor. The ANOVA revealed significant main effects of Block Length ($F(1,77) = 18.80, p < 0.001, \eta_p^2 = 0.1960$, Test Format ($F(1,77) = 42.77, p < 0.001, \eta_p^2 = 0.357$), and a marginal effect of Age ($F(1,77) = 3.48, p = 0.066, \eta_p^2 = 0.043$). These main effects were qualified by a significant Block Length x Test Format interaction ($F(1,77) = 8.49, p < 0.005, \eta_p^2 = 0.099$) and Test Format x Age interaction ($F(1,77) = 5.38, p < 0.05, \eta_p^2 = 0.065$). To investigate how the effects of Block Length and Age varied across Test Format, I conducted follow-up Block Length x Age ANOVAs separately for Forced Choice and Yes/No Test performance.

In the Forced Choice Test, a significant main effect of Block Length was detected ($F(1,77) = 26.57, p < .001, \eta_p^2 = 0.257$) that did not differ with age ($F(1,77) = 1.59, p = .211, \eta_p^2 = 0.020$). Critically, the effect of age on recognition memory performance was not significant ($F < 1$), and this was true for both short ($t < 1$) and long ($t(77) = 1.37, p = .17, d = 0.31$) block lengths. In contrast, Yes/No performance did not decline significantly as block length increased ($F < 1$), and this was true across both age groups, with no evidence of an interaction ($F(1,77) = 1.67, p = .20, \eta_p^2 = 0.021$). However, significant age differences in Yes/No performance persisted ($F(1,77) = 7.63, p < .01, \eta_p^2 = 0.09$).

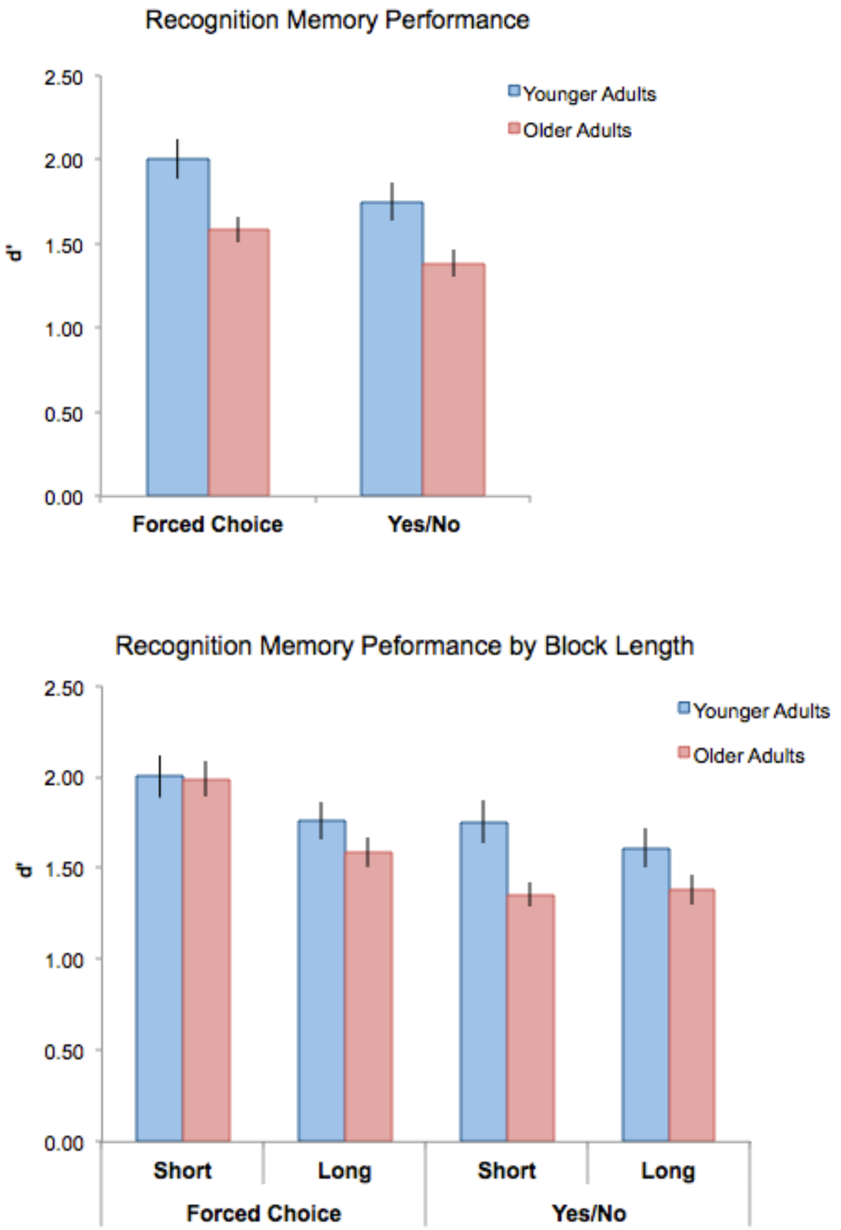

Figure 3: *(Top) Recognition memory performance (d-prime) following study of an equal number of items across age groups (180 objects) in Experiment 2. Older adults exhibited deficits in performance across both the Forced Choice and Yes/No test formats. (Bottom) Recognition memory performance following short (YA: 180 objects; OA: 60 objects) and long (YA: 300 objects; OA: 180 objects) study-test blocks in each test format. No age differences were observed in Forced Choice performance, whereas older adults exhibited significant declines in Yes/No performance.*

Discussion

In Experiment 2, I explored the effect of manipulating the presence of feature-level interference on memory performance across test formats. I predicted that reducing this interference would enhance older adults' performance in the Forced Choice test by improving the efficacy of representations for discriminating between targets and lures. Indeed, my manipulation of list length, whereby older individuals experienced lower levels of interference than younger individuals by virtue of studying fewer items, eliminated age differences in Forced Choice performance, whereas age differences in Yes/No recognition persisted. This pattern of results is consistent with separable contributions of representational quality and impaired strategic retrieval processes to age-related increases in false recognition, with the degree to which each factor influences performance dependent on the task demands associated with the test format.

In particular, the influence of interference on Forced Choice performance is consistent with the proposal that object-level stimulus representations become compromised with age, leading to a greater susceptibility to interference from lower level features that are shared amongst common everyday objects (Burke et al., 2010, 2011; Ryan et al., 2012; Yeung et al., 2013). When this interference is reduced, lower level representations become more effective in successfully disambiguating exemplars with overlapping features, resulting in significant improvements in discrimination ability (Bartko et al., 2010; McTighe et al., 2010; Burke et al., 2011). Notably, when examining conditions analogous to those in Experiment 1, wherein older adults faced an equivalent amount of interference as younger adults, age differences were again observed in both test formats, replicating my prior results. In contrast, I found no evidence that Yes/No recognition performance was impacted by the presence of interference, at least across the list lengths considered here. This may reflect the high demands this test format places on strategic retrieval processes (e.g., recall-to-reject), such that the ability to execute these processes places an upper boundary on performance, constraining the degree to which older adults can improve. The observation that older adults did not exhibit any benefits of reduced interference in this test format is consistent with age-related impairments in engaging strategic, recollection-based retrieval processes (Gallo et al., 2006; 2007; Cohn et al., 2008; Luo & Craik, 2009).

Neuropsychological Assessment

The results of Experiments 1 and 2 suggest that two factors may contribute to age-related decline in recognition memory: reductions in the quality of stimulus representations and impairments in strategic retrieval processes. Furthermore, they lend support to the idea that representational quality is a critical determinant of Forced Choice performance, whereas the ability to make accurate Yes/No discriminations is constrained by the ability to initiate strategic control processes to retrieve and evaluate stored representations in the absence of environmental support. If this is indeed the case, individual differences in these component processes may be differentially related to older adults' recognition memory performance across test formats. For example, previous studies have observed a relationship between standardized tests of recall and older adults' performance in Yes/No recognition with similar foils (Toner et al., 2009; Holden et al., 2014; Migo et al., 2014), likely due to the similar demands these tests place on strategic retrieval and monitoring of stored representations in the absence of retrieval support.

To investigate this possibility in the current study, I administered a battery of neuropsychological tests to a subset of older adults who participated in Experiments 1 and 2, in order to characterize individual differences in representational quality, recall ability, and executive function. I then examined the relationship between these scores and older adults' performance across test formats. I predicted that older adults with higher indices of representational quality would exhibit superior Forced Choice performance, as this factor is expected to be both necessary and sufficient to support simultaneous discriminations between exemplars. In contrast, older adults scoring higher in measures of recall performance and executive function were expected to exhibit an enhancement in Yes/No recognition performance, which places substantial demands on retrieval and evaluation of stored details, as well as attentional control processes and online maintenance of information in working memory.

Method

Participants

Forty-two older adults were tested, 20 who completed Experiment 1 and 22 who completed Experiment 2. The older adults from each experiment did not differ with respect to mean age, years of education, or Shipley Vocabulary Scores (all $t < 1$). The groups did differ in their scores on the Montreal Cognitive Assessment, however both groups performed well within the normal range (Exp. 1: $M = 28.25$, $SD = 1.12$; Exp. 2: $M = 27.23$, $SD = 1.69$; $t(40) = 2.29$, $p < .05$, $d = 0.724$). The individuals from each experiment were also matched on object recognition memory performance across test formats (all $p > .20$) and were combined for all subsequent analyses. A summary of the demographic information can be found in Table 2.

Neuropsychological Battery & Procedure

All participants completed a battery of neuropsychological tests assessing memory, executive function, and perception. These included the Logical Memory and

Paired Associates subtests from the Wechsler Memory Scale (4th Edition; WMS-IV, Wechsler, 2009), the Rey-Osterrieth Complex Figure Test (Osterrieth, 1944), the Verbal Fluency and Trails A & B subtests from the Delis-Kaplan Executive Function System (D-KEFS, Delis, Kaplan & Kramer, 2001), and the Digit Span subtest from the Wechsler Adult Intelligence Scale (4th Edition; WAIS-III, Wechsler, 2008). Participants additionally completed a complex visual discrimination task using stimuli developed by Barense and colleagues (2012; see also Newsome et al., 2012 and Ryan et al., 2012). In this task, participants are simultaneously presented with two novel objects and decide if they match or do not match. Critically, when these objects share multiple overlapping features (e.g., high ambiguity trials), convergent evidence from patients with PRC lesions (Barense et al., 2012) and neuroimaging studies in older (Ryan et al., 2012) and younger (Barense et al., 2012) adults indicate that successful performance relies on conjunctive object-level representations supported by the PRC to resolve feature level ambiguity between exemplars.

Table 2: Demographics & Memory Performance of Older Adults who completed Neuropsychological Testing

	Experiment 1	Experiment 2
N	20	22
Age	71.55 (4.51)	70.27 (5.76)
Education	18.15 (7.22)	17.23 (3.15)
Shipley	37.20 (2.63)	37.09 (1.74)
MoCA	28.25 (1.12)	27.23 (1.69)*
Forced Choice	1.51 (.64)	1.53(.41)
Yes/No	1.31 (.65)	1.16 (.43)

Scores on each of these subtests were normalized and the *z* scores averaged to create three different composite scores for each individual: a Representational Quality score, a Recall Performance score, and an Executive Function score. The Representational Quality score consisted of performance on the high ambiguity condition of the visual discrimination task. The Recall Performance score comprised immediate and delayed recall scores from the Logical Memory, Paired Associates, and Rey Complex Figure tests. The Executive Function score comprised Verbal Fluency, Trails B, and Digit Span scores. The group was median split on each composite score to divide participants into high and low scoring groups in each of the three factors. One-way between-participants analyses of variance confirmed that the high and low scoring groups differed significantly on their respective composite scores (Representational Quality Groups: $F(1,41) = 74.69$ $p < .001$; Recall Performance Groups: $F(1,41) = 76.13$, $p < .001$; Executive Function Groups: $F(1,41) = 49.34$ $p < .001$). A full summary of the demographic information and composite scores for each group can be found in Table 3.

Results

To assess the potential influence of Representational Quality, Recall Performance, and Executive Function on recognition memory performance (see Figure 4), I submitted participants' *d'* scores from Experiments 1 and 2 to 2 x 2 mixed ANOVAs with Test Format as a within-subjects factor and Group (high vs. low scores on a specific neuropsychological test) as a between-subjects factor. For those participants who completed Experiment 2, performance on the 180 item block was used to calculate their *d'* scores to ensure that performance measures were based on comparable experimental conditions across participants. In instances where composite scores were correlated with one another, which was the case for Representational

Quality and Recall Ability ($r = 0.375, p < .05$), as well as Recall Ability and Executive Function ($r = 0.545, p < .001$), these scores were included as covariates in the relevant ANOVA to account for their possible effects on performance.

Table 3: Characteristics of Older Adults as a Function of Neuropsychological Group

	Recall Ability Group		Executive Function Group		Representational Quality Group	
	High	Low	High	Low	High	Low
N	21	21	21	21	21	21
Age	68.2(4.3)	73.6(4.7)***	68.9(5.3)	72.9(4.3)*	70.8(4.4)	71.0(6.0)
Education	18.6(3.2)	16.7(7.0)	19.1(6.4)	16.2(3.8)	17.3(3.3)	18.0(7.0)
Shipley	38(1.3)	36.3(2.6)**	37.8(1.4)	36.5(2.6)	37.3(2.3)	37(2.1)
MoCA	28.1(1.3)	27.3(1.7)	28(1.3)	27.5(1.7)	28(1.1)	27.5(1.9)
Recall Ability	.54(.42)	-.54(.43)***	.26(0.6)	-0.26(.7)*	.11(.59)	-.11(.78)
Executive Function	.31(.62)	-.31(.79)**	.56(0.4)	-.56(0.6)***	.12(.77)	-.12(.76)
Rep Quality	.43(.76)	-.43(1.0)**	.14(1.0)	-.14(1.0)	.75(.42)	-.75(.83)***
Forced Choice *d'*	1.85(.45)	1.19(.40)***	1.78(.42)	1.26(.53)**	1.67(.53)	1.37(.51)*
Yes/No *d'*	1.53(.49)	.94(.47)***	1.46(.52)	1.02(.52)**	1.28(.59)	1.20(.54)

Note: *Standard deviations are indicated in parentheses next to mean values. Asterisks indicate a difference between low and high scoring groups (* = p < .05, ** = p < .10, *** = p < .001). MoCA = Montreal Cognitive Assessment.*

The results indicated that older adults scoring higher in Recall Ability performed significantly better than those individuals in the low scoring group ($F(1,40) = 23.66, p < 0.001, \eta_p^2 = 0.372$) across both test formats ($F < 1$). This effect remained significant when Representational Quality and Executive Function scores were taken into account ($F(1,40) = 5.71, p < 0.05, \eta_p^2 = 0.144$). Similarly, I observed a significant difference in memory performance between the High and Low Executive Function groups ($F(1,40) = 11.07$, $p < 0.005$, $\eta_p^2 = 0.217$) across test formats ($F < 1$), and this effect remained when Recall Ability was included as a covariate ($F(1,40) = 4.35$, $p < 0.05$, $\eta_p^2 = 0.100$).

In contrast, older adults in the high and low Representational Quality groups did not differ with respect to overall memory performance ($F < 1$). Instead, I observed a significant Test Format x Group interaction ($F(1,40) = 4.42$, $p < 0.05$, $\eta_p^2 = 0.100$), which remained significant when Recall Score was included as a covariate ($F(1,40) = 4.36$, $p < 0.05$, $\eta_p^2 = 0.101$). This interaction reflected a selective impact of representational quality on Forced Choice performance ($t(40) = 2.02$, $p < .05$, $d = 0.638$), that was not observed in Yes/No performance ($t < 1$).

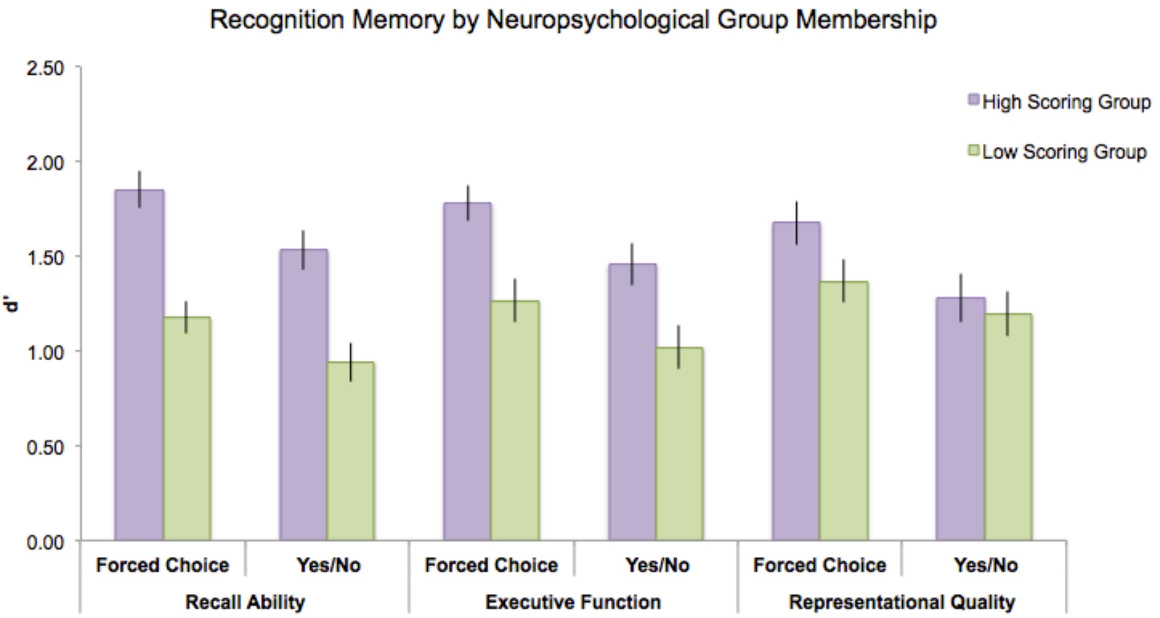

Figure 4: Recognition memory performance (d-prime) in the Forced Choice and Yes/No Tests in older adults divided into high and low scoring groups based on neuropsychological test performance. Older adults with higher scores in Executive Function and Recall Ability performed significantly better across test formats than older adults with lower scores in these measures. Older adults with higher scores in Representational Quality performed significantly better than older adults with lower scores in this measure in the Forced Choice test, but these groups did not differ in Yes/No test performance.

I also predicted that any benefits gained by the presence of retrieval support would be constrained by the quality of object representations. Accordingly, I computed a difference score quantifying the memory enhancement associated with the Forced Choice Test as compared to the Yes/No Test (see also Westerberg et al., 2013). I then assessed whether the size of this mnemonic benefit varied according to group membership for the three neuropsychological tests. This analysis revealed that those participants in the high Representational Quality group benefited significantly more from the presence of retrieval support than did the low Representational Quality group ($t(40) = 2.10$, $p < .05$, $d = 0.664$), whereas there was no significant difference in this benefit between high and low scoring participants in the Recall Performance or Executive Function groups (all $t < 1$).

Discussion

Consistent with my first prediction, older adults with higher indices of representational quality exhibited superior Forced Choice performance relative to those with lower scores, and exhibited larger benefits of retrieval support. This result is consistent with the idea that conjunctive object-level representations, which were critical to support performance in the selected measure of representational quality, are both necessary and sufficient to support judgments of the relative familiarity between exemplars with overlapping features. Accordingly, the quality of these representations not only constrained Forced Choice performance, but also the degree to which older adults could benefit from the simultaneous presentation of targets and lures relative to the item-wise presentation in the Yes/No test.

In contrast, I found that representational quality was not a good predictor of performance in the Yes/No test. This observation is consistent with the proposal that variations in representational quality do not have a direct impact on Yes/No performance, perhaps owing to the additional controlled retrieval processes that are critical to support performance. Consistent with this possibility, and my second prediction, older adults who scored higher on measures of both recall ability and executive function, which are thought to support one's ability to retrieve and evaluate stimulus representations in the absence of retrieval support, performed significantly better in the Yes/No test. Note however that these older adults also performed significantly better on the Forced Choice test. Although not predicted, this pattern suggests that the use of recollection-based retrieval strategies may not be essential to support accurate Forced Choice decisions (e.g. Holdstock et al., 2002; Migo et al., 2009), but can nevertheless enhance one's performance when they are available.

General Discussion

The primary goal of the current investigation was to explore the degree to which age-related declines in representational quality and strategic retrieval processes contribute to increases in false recognition among older adults. To this end, I assessed older and younger adults' recognition memory performance in both Forced Choice and Yes/No test formats on the basis that performance in each test is differentially sensitive to these factors, as suggested by prior work (e.g. Holdstock et al., 2002; Migo et al., 2009; Westerberg et al., 2013). The results revealed that age-related increases in false recognition were not only evident in the context of the Yes/No test, wherein demands on recollection-based retrieval processes are high, but also in the Forced Choice test, where such demands are reduced. This pattern suggests that impaired retrieval processes alone cannot fully account for increases in false recognition, and provides evidence for a role of age-related declines in representational quality. In support of this proposal, I found that reducing perceptual interference substantially improved Forced Choice performance, whereas performance in the Yes/No test remained unchanged, with age differences in performance persisting. This pattern cannot easily be explained by a single factor, and suggests that declines in both representational quality and strategic retrieval processes contribute to age-related increases in false recognition.

This interpretation is further supported by the current neuropsychological data, which revealed that individual differences in representational quality impacted Forced Choice performance, but not Yes/No performance. Furthermore, recall ability and executive function influenced performance across both test formats. Relationships with respect to Yes/No recognition performance and more general recall ability in older adults have been reported before (Toner et al., 2009; Holden et al., 2014; Migo et al., 2014), and the current data extends this work by identifying a similar relationship for executive function. The present study is the first to identify an association between recognition memory performance and a measure of representational quality defined solely on the basis of a simultaneous perceptual discrimination task that does not incur any mnemonic demands, but has been shown to require complex, object-level representations (Barense et al., 2012). This finding lends support to the interpretation that variations in representational quality critically impact one's ability to make judgments of relative familiarity between targets and foils when they share a high degree of feature overlap. Moreover, this observation adds to a growing body of work providing evidence for a decline in the availability of conjunctive, object-level representations with age (Burke et al., 2010; 2011; Ryan et al., 2012; Newsome et al., 2012; Yeung et al., 2013), and highlights the impact this has on memory performance.

Interestingly, the observed relationship between these cognitive measures and memory performance across test formats is highly consistent with previous findings of a relationship between memory performance in the same two recognition tests and measures of regional brain volume in patients with Mild Cognitive Impairment and more advanced Alzheimer's disease (Westerberg et al., 2013). Specifically, PRC volume was selectively related to Forced Choice performance, as well as to the size of the benefit gained by retrieval support, whereas hippocampal volume was related to performance across test formats (Westerberg et al., 2013). Although I did not measure brain structure in the present experiments, the close correspondence between my findings and those of Westerberg and colleagues suggests that the measures used here may be sensitive to individual variability in the integrity of these brain regions among older adults. Specifically, the current data are consistent with the proposal that the measure of representational quality used here, which has been previously been related to PRC activity in both older and younger adults (Ryan et al., 2012; Barense et al., 2012), may be an index of individual differences in PRC function among older adults in the present sample. Similarly, the free recall and executive function tasks used in the current battery are thought to be sensitive to hippocampal and prefrontal function, respectively, and may reflect variability in the integrity of these brain regions in the elderly population.

Although I cannot make definitive statements regarding the brain regions contributing to performance in each of the neuropsychological measures, the observed relationship between these cognitive factors and memory performance is nevertheless consistent with computational models of the neural mechanisms supporting recognition memory across test formats when targets and foils are highly similar. Specifically, previous modeling and empirical studies suggest that performance in the Yes/No test requires the involvement of recollection and depends critically on the hippocampus, whereas Forced Choice performance can largely be supported by familiarity-based judgments that rely on intact PRC (Holdstock et al., 2002; Migo et al., 2009; Norman, 2010). The current data are consistent with such a distinction, but also extend existing models by further specifying the role that PRC may play in supporting familiarity-based judgments in the Forced Choice test, namely by maintaining complex, object-level representations that are critical for discriminating between exemplars sharing overlapping features.

This interpretation is based upon the correspondence between the present findings and the predictions made by the representational-hierarchical view of object recognition (Cowell et al., 2006; Bussey & Saksida, 2007). Specifically, this view proposes that object representations are organized hierarchically in the ventral visual stream, with simple feature represented in more posterior regions, and increasingly complex conjunctions of features represented along the ventral stream towards PRC, which is thought to support unique, object-level representations (Cowell et al., 2006). These representations are critical for resolving feature ambiguity in both perceptual and mnemonic discriminations between objects sharing overlapping features (Bussey & Saksida, 2007). Thus, when the integrity of PRC is compromised, this is thought to lead to increased reliance on lower level representations of simple features (e.g. colour, shape) and their conjunctions, which are not unique to each stimulus, but often shared by targets and foils. Such representations are less likely to support successful discriminations between exemplars, leading to increased rates of false recognition (e.g., McTighe et al., 2010). Furthermore, this view also predicts that reducing feature-level interference should lead to improved discrimination ability by increasing the efficacy of intact, lower level representations for making accurate discriminations (Cowell et al., 2006; McTighe et al., 2010). These predictions accord well with the behavioural performance exhibited by older adults in the current experiments.

Not only did I observe age-related deficits in discriminating between targets and foils with overlapping features in the Forced Choice test, but I also discovered that reducing the amount of study phase interference from lower-level features enhanced older adults' discrimination ability and eliminated age differences in Forced Choice performance. These findings lend further support to previous reports of age-related declines in representational quality (Burke et al., 2010; Ryan et al., 2012; Newsome et al., 2012; Yeung et al., 2013), which may be indicative of altered PRC function in advanced age (Ryan et al., 2012; Burke et al., 2014). Moreover, the present results complement a growing body of work identifying the benefits of reducing feature-level interference on memory and perception in both humans (Barense et al., 2012; Newsome et al., 2012;) and animals (McTighe et al., 2010; Bartko et al., 2010; Burke et al., 2011; Romberg et al., 2012) with compromised PRC integrity. Interestingly, I found that when exposed to considerably higher levels of feature-based interference than older adults, younger adults also exhibited declines in Forced Choice performance. This pattern may reflect potential boundary conditions in the intact representational system's ability to cope with interference. Critically, the observation that older adults exhibited declines in Forced Choice performance in the context of significantly smaller amounts of interference provides evidence for a compromised representational system with age that leads to greater vulnerability to interference, contributing to age-related increases in false recognition.

However, the current results suggest that declines in representational quality cannot fully account for age differences in Yes/No recognition, which persisted even under conditions of reduced interference. This observation is consistent with numerous reports of elevated rates of false recognition among older adults in Yes/No recognition tests with similar foils (Koutstaal, 2003; Toner et al., 2009; Yassa et al., 2011; Holden et al., 2013), as well as evidence that age differences in such tests persist irrespective of the number of intervening items between study and test (Stark et al., 2015). Together, this evidence suggests that Yes/No recognition performance is less sensitive to manipulations of interference. This may be due to the additional demands on strategic retrieval processes associated with the item-wise presentation of targets and foils, which may constrain older adults' performance in this test. Indeed, this proposal is consistent with previous work identifying disproportionate age-related memory impairments under test conditions that place significant demands on the recollection of specific details from memory in order to reject lures that share a high level of familiarity (Gallo et al., 2006; 2007; Cohn et al., 2008; Luo & Craik, 2009).

Such increases in false recognition are often associated with age-related changes in hippocampal (Dennis, Kim, & Cabeza, 2008; Bowman & Dennis, 2015) and prefrontal function (Mitchell, Raye, Johnson, & Greene, 2006; McDonough, Wong, & Gallo, 2013) during retrieval, which are thought to reflect impaired reinstatement and monitoring of stored representations, respectively. Previous work has also suggested that impaired Yes/No recognition memory with similar foils may reflect age-related declines in hippocampal pattern separation (Yassa et al., 2011). In particular, it has been proposed that greater dissimilarity between inputs may be required for successful pattern separation in older relative to younger adults, leading to an increased incidence of false recognition to similar lures. This proposal is also consistent with the current data, suggesting this mechanism may contribute to the observed age differences in performance. However, it is unlikely that this factor alone can explain performance in Yes/No recognition. In particular, the current observation that older adults scoring higher in standardized measures of both free recall and executive function exhibited substantial enhancements in Yes/No recognition suggests that maintenance of both hippocampal and prefrontal function is critical to support performance on this task.

Despite the current evidence for age-related declines in recollection-based retrieval processes and representational quality, I cannot rule out the potential contribution of age-related impairments at encoding. For example, there is evidence to suggest that older adults are less likely to use encoding strategies to support elaborative and distinctive encoding of event details, and that instructions to adopt such strategies can significantly enhance memory performance in older adults (Craik & Rose, 2012). Thus, it is possible that younger adults were more likely than older adults to use strategies to facilitate memory for specific stimulus details, leading to enhanced memory performance. In fact, the performance enhancement among older adults with better executive function may have arisen due to greater availability of attentional control resources to support strategic processes at encoding or retrieval, thereby improving performance. Although it is certainly possible that age differences during encoding may contribute to the current results, there are several reasons why I think it unlikely that this factor can wholly account for the pattern of results observed here.

First, I used an incidental encoding task to encourage comparable processing of images by older and younger adults, as this has previously been shown to enhance the similarity of encoding operations across age groups (e.g., Logan et al., 2002). Indeed, previous experiments that included attentional manipulations at encoding to encourage greater attention to stimulus detail failed to eliminate age differences in performance (Koutstaal et al., 1999; Stark et al., 2015), suggesting that additional factors contribute to this deficit. Moreover, the current findings parallel previous evidence observed in studies of aged rats and monkeys (Burke et al., 2010; 2011), suggesting that age-related changes in representational quality arise even when the use of more elaborative, meaning-based strategies are not available to either age group. Finally, it is unlikely that the specific pattern of results, namely a consistent age-related reduction in Yes/No performance, coupled with variable age differences in Forced Choice performance, could be explained solely by age differences in encoding processes. Nevertheless, the present data do not discount the potential utility of encoding strategies that provide an alternative means of storing information that can disambiguate targets and lures, thereby reducing reliance on intact perceptual representations that appear to decline with age.

However, the current results suggest that even in the absence of such explicit strategies, older adults' ability to make fine-grained mnemonic distinctions between highly similar exemplars can be improved by combining environmental support at retrieval with a reduction in perceptual interference. Taken together, the present findings indicate that age-related increases in false recognition arise not only due to impairments in controlled retrieval processes, but also declines in representational quality. These results converge with a growing body of work in aged humans and animals, and suggest that exploring the relationship between complex perception and memory may be critical for understanding and ameliorating age-related declines in memory performance.

In summary, the results of these experiments lend further support to the proposal that age-related declines in episodic memory, and in particular the ability to discriminate between highly similar events, can be attributed to both declines in representational quality, and impairments in controlled retrieval processes. This was demonstrated behaviourally by manipulating interference and retrieval support, therefore varying demands on representational quality and controlled retrieval, respectively. Further support for this hypothesis was obtained through the observation that independent measures of representational quality, recall ability, and executive function, which tap into both of these factors, were indeed related to memory performance across older adults. Importantly, these tests are thought to reflect the function of underlying brain areas that are important for supporting these functions, in particular medial temporal and prefrontal regions, consistent with the idea that age-related decline in representational quality and controlled retrieval have a basis in individual differences in regional brain function. This possibility is explored in the next chapter using univariate and multivariate analysis of fMRI data.

Chapter 4

Representational quality and cortical reinstatement during associative memory: A multivariate fMRI investigation

Introduction

The findings of the previous two chapters implicate multiple factors in age-related episodic memory decline, including reductions in the quality of stimulus representations during encoding and impairments in the ability to strategically retrieve and evaluate stored details at test. Moreover, the neuropsychological test results from Chapter 3 suggest that individual differences in brain structure and function of older adults may contribute to these deficits. In Chapter 4, I seek direct neural evidence for age-related changes in representational quality and strategic retrieval processes using functional magnetic resonance imaging (fMRI). Much of the previous research aimed at addressing these questions has applied univariate analysis to fMRI data to assess age differences in regional BOLD activity during encoding and retrieval. These studies have identified age differences in the magnitude and localization of BOLD activity that are suggestive of differences in representational quality and strategic retrieval (see Grady, 2013 for review).

During encoding, older adults typically demonstrate reduced activity in posterior cortical regions associated with sensory processing, coupled with increased activity in the prefrontal cortex (Grady et al., 1995; Grady et al., 2003; Gutchess et al., 2005; Dennis et al., 2008). This pattern suggests that older adults are less likely to encode specific event details, but also suggests that older adults might be engaging an alternative, compensatory encoding strategy. More direct evidence for age-declines in representational quality has come from studies that involve viewing stimuli from different visual categories, which have observed age-related reductions in neural specialization and selectivity in ventral visual cortex (Park et al., 2004; Goh et al., 2010; Burianova et al., 2013). In these studies, younger adults selectively recruited different brain regions when viewing different visual stimulus categories (e.g., faces versus houses), older adults recruited the same regions for all stimulus categories.

During retrieval, evidence for age-related reductions in strategic retrieval processes has also been identified. For example, older adults typically exhibit reduced BOLD activity relative to younger adults in medial temporal and posterior representational regions during retrieval, which is often coupled with increased activity in the prefrontal cortex (Grady et al., 2005; Gutchess et al., 2005; Davis et al., 2008). Such age differences in the localization of neural recruitment is often thought to reflect a shift in retrieval strategies with age, with a decreased likelihood of engaging recollection-based strategies that involve reinstating specific event details, perhaps towards more familiarity-based retrieval strategies. This shift in retrieval processes may result from inadequate neural resources to support strategic retrieval. For instance, younger adults exhibit demand-dependent recruitment of prefrontal cortex, where prefrontal activity tracks requirements for strategic, recollection-based retrieval, whereas older adults often exhibit persistent elevations in prefrontal activity even at low levels of demand (Giovanello & Schacter, 2012; McDonough et al., 2013). This observation is thought to reflect reduced neural efficiency in older adults, such that more neural resources must be recruited to accomplish a simple task, leaving little additional resources available when the task demands increase.

Taken together, the results of these studies are suggestive of age-related decline in the quality of event representations, and in the ability to engage strategic retrieval processes. However, because this evidence comes from observations of relative increases or decreases in regional BOLD activity, they can be difficult to interpret. In particular, age-related increases in prefrontal activity are sometimes considered compensatory in nature when positively related to performance (e.g., Cabeza et al., 2002), but at other times are considered evidence for dedifferentiation and neural inefficiency (Cabeza, 2002; Grady, 2013). Moreover, recent work indicates that task-relevant information may be coded not through the overall magnitude of activation of the region, but through specific patterns of activity across voxels within a given region (Mur, Bandettini, & Kriegeskorte, 2009; Jimura & Poldrack, 2012). Thus, age-related increases or decreases in regional BOLD activity do not tell us whether, or how, the representations and computations supported by these regions differ between older and younger adults. Similarly, even in the absence of age differences in regional BOLD activity in a given region, substantial differences may be present in the quality or nature of the information carried in distributed activity patterns. These limitations in univariate analysis of fMRI data can be mitigated by complementing this approach with multivariate pattern analysis of fMRI data, which can provide insight into the information carried in distributed patterns of neural activity throughout the brain (Kriegeskorte, Mur, & Bandettini, 2008; Kriegeskorte & Kievit, 2013).

In particular, multivariate fMRI analysis can be used to assess the distinctiveness of neural representations associated with different events during encoding. Previous work has provided evidence that patterns of neural activity across voxels can reliably distinguish between different cognitive operations (Johnson, McDuff, Rugg, & Norman, 2007; Gordon, Rissman, Kiani, & Wagner, 2014), visual stimulus categories (Carp, Park, Polk, & Park, 2011; Kuhl, Rissman, & Wagner, 2012), or even individual stimulus exemplars (Kriegeskorte et al., 2008; St-Laurent et al., 2014) during perception and encoding. Similarly, multivariate analyses can be used to assess the degree to which an individual retrieves specific perceptual and contextual details from encoding to support memory judgments, which is thought to be indicative of the engagement of a recollection-based retrieval strategy. Previous studies have revealed reinstatement of encoding-related activity patterns associated with stimulus category (Polyn, Natu, Cohen, & Norman, 2005) and task context (Gordon et al., 2013), and as well as specific events (Staresina, Henson, Kriegeskorte, & Alink, 2012; Kuhl & Chun, 2014; Tompary, Duncan, & Davachi, 2016; Wing, Ritchey, & Cabeza, 2015) during memory retrieval. Overall, these studies have found that increased neural distinctiveness during encoding, as well as greater reinstatement of encoding-related activity during retrieval, are associated with successful memory retrieval, and tend to scale with the degree to which an event is recollected with high confidence and vividness (e.g., Johnson et al., 2007; Kuhl & Chun, 2014; Wing et al., 2015).

Taken together, this evidence suggests that multivariate analysis of fMRI data can provide sensitive measures of both the differentiation of event representations during encoding, as well as the degree to which these representations are reactivated during retrieval, making this approach well suited to the current exploration of how aging affects each of these variables. However, few experiments have applied such analyses to older adults' fMRI data to date, and thus far the results have been mixed. With respect to differentiation of stimulus representations during perception, previous work has identified significant age-related reductions in the distinctiveness of neural activity patterns in ventral visual cortex during passive viewing of visual stimuli from different categories (Carp et al., 2011; Johnson et al., 2015). In contrast, other work has found that age differences in the distinctiveness of neural representations are not evident during encoding, but are robust during retrieval (St-Laurent et al., 2014;

Abdulrahman, Fletcher, Bullmore, & Morcom, 2015). For example, St-Laurent and colleagues (2014) identified significant reductions in the reinstatement of stimulus-specific patterns of encoding-related activity during retrieval, despite negligible differences in the distinctiveness of stimulus representations during encoding. Similarly, Abdulrahman and colleagues (2015) identified significant age-related decline in the ability of neural activity patterns during memory retrieval to differentiate between task contexts, despite the absence of age differences in the distinctiveness of neural representations associated with two different contexts during encoding. Finally, other work has failed to identify age differences in the distinctiveness of neural activity patterns during encoding or during retrieval (Wang, Chattin, Thompson, & Tomsky, 2016).

The large degree of variability in results across these experiments can likely be explained by differences in experimental design that are likely to impact the presence of age differences in neural measures of representational specificity and cortical reinstatement. For example, age differences during encoding tend to be identified in paradigms wherein more similar conditions are contrasted, such as different categories of visual stimuli (e.g., faces versus houses, objects versus scenes), and have been absent when comparison conditions are more distinct (e.g., words versus pictures; Wang et al., 2016), or when task-based comparison are made (e.g., shallow versus deep semantic encoding judgments; Abdulrahman et al., 2015). Thus, differences in the results obtained across experimental paradigms do not necessarily imply differences in the quality of stimulus representations among older adults across experiments, but could instead reflect differences in the similarity between comparison conditions.

Similarly, age differences in the reinstatement of encoding-related activity during retrieval have been primarily observed when the memory test places demands on retrieval of specific details with minimal support from the environment (e.g., cued recall; St-Laurent et al., 2014; Johnson et al., 2015), or strategic retrieval processes (e.g., adopting a strategic retrieval orientation: Abdulrahman et al., 2015). In contrast, age differences were not observed during a test assessing memory for single items that varied in event distinctiveness (e.g., presented as pictures versus words: Wang et al., 2016), which likely reduced demands on strategic retrieval processes (Gallo et al., 2007). Together, this evidence suggests that age differences in reinstatement measures tend to be more pronounced under conditions that place demands on retrieval processes that are themselves impaired with age. Thus, although these previous findings appear highly variable on the surface, they may not be inherently contradictory. Nevertheless, the degree to which differentiation and reinstatement of neural representations during encoding and retrieval varies with age, particularly on a trial-wise, event-specific basis, remains unclear.

The Present Experiment

The current fMRI investigation sought to further characterise age differences in the distinctiveness of stimulus representations during encoding, as well as the degree to which encoding-related activity patterns are reinstated during retrieval. To this end, participants were scanned while completing a paired associates memory task, which involves encoding and retrieving word-picture pairs in a recombined recognition test. Older adults typically exhibit significant deficits in performance on such tasks, often characterised by an intact hit rate coupled with an increased false alarm rate (Naveh-Benjamin, 2000; Castel & Craik, 2003; Cohn et al., 2008). These age differences are thought to arise due to the significant demands this task places on both the formation of highly specific event representations, as well as strategic retrieval and monitoring of specific event details, making the task well suited for identifying neural markers of age-related changes in these factors.

Pattern similarity analysis was applied to fMRI data acquired as participants encoded and retrieved trial-unique adjectives paired with one of eight images. Each image was presented multiple times throughout the experiment, each time paired with a different adjective (e.g., an image of an umbrella might on different trials be paired with the adjectives 'sparkling', 'golden', etc.). The images were organized in a hierarchical categorical structure. At the highest level, they could be divided into two categories, objects and scenes. These two categories could then each be divided into two subcategories: living and non-living objects, and indoor and outdoor scenes. Finally, each of these subcategories consisted of two specific image exemplars. This structure supported the creation of word-picture pairs that varied in their relatedness; some events were distinct from one another, and could be distinguished on the basis of general category or subcategory information, whereas other events were highly similar, and could only be distinguished on the basis of the unique adjective pairing. This enabled me to examine whether age differences in neural distinctiveness are more likely to emerge in the context of distinguishing between highly similar events, relative to events that are more distinct.

Memory for word-picture pairs was then assessed using a recombined recognition test. Unlike cued-recall tests, which can also be used to evaluate memory for associations between items, this test contains two trial types that vary in their demands on strategic retrieval processes. These include intact trials, wherein the tested word-picture pairing is identical to that which was studied previously, and recombined trials, wherein both the word and picture were studied previously, but were not originally paired together. Whereas intact pairs provide a congruent cue that can facilitate retrieval of the target event, therefore providing a high level of retrieval support, recombined pairs provide an incongruent cue, thus placing significant demands on self-initiated, strategic retrieval of event details with minimal support from the environment. In particular, successful rejection of recombined pairs is thought to involve recall and evaluation of the original paired associate in order to reject the novel combination (Cohn & Moscovitch, 2007). Previous work has identified a different network of brain regions involved in recall-to-accept strategies as compared to recall-to-reject (Bowman & Dennis, 2016). This design enables me to assess whether the degree to which encoding-related activity is reinstated during retrieval varies according to demands on strategic retrieval processes across trial types (e.g., intact versus recombined).

Previous behavioural findings suggest that aging is associated with a decline in the ability to implement a recall-to-reject strategy in response to familiar lures, whereas the ability to accurately endorse studied items/intact pairs remains largely intact (Cohn et al., 2008; Chapter 3). However, it remains unclear whether this pattern represents a cue-dependent impairment in the ability for older adults to retrieve specific event details. For example, it may be that older adults can retrieve event details when this is supported by a strong retrieval cue (e.g., intact recall-to-accept), but not in response to an incongruent cue (e.g., impaired recall-to-reject). In contrast, this pattern may simply represent an increased reliance on familiarity-based responding, which can support accurate responses to intact pairs, but results in increased false alarms to recombined pairs. A third, not mutually exclusive, explanation for this pattern, is that older adults may rely on retrieval of more general aspects of previous events, rather than highly specific event details (Koutstaal &

Schacter, 1997; Koutstaal et al., 1999), which is sufficient to support hits to intact pairs, but not sufficient to support a recall-to-reject strategy. The present study aims to tease apart these possibilities.

Summary of Aims & Predictions

In summary, the current fMRI study sought to characterise age-related changes in the quality of stimulus representations during encoding, and the ability to recall specific event details to support recognition decisions during retrieval. In particular, it aimed to explore the effects of age on two properties of neural representation: i) the degree to which pattern similarity between events is sensitive to differences in stimulus relatedness during encoding, and ii) the degree to which event-specific or category-level patterns of encoding-related activity are reinstated at retrieval during hits to intact pairs and correct rejections of recombined pairs.

To address the first question, pattern similarity analysis was used to assess the event-level similarity between neural activity patterns during encoding, comparing events that ranged from highly related (e.g., sharing the same exemplar, Sparkling Umbrella versus Golden Umbrella) to more distinct (e.g., including images from different categories, Sparkling Umbrella versus Flowery Office). This analysis was conducted in a single region of interest, the ventral visual cortex, which has previously been identified as sensitive to category (Carp et al., 2011; Kuhl et al., 2012) and exemplar information of visual stimuli (Kriegeskorte et al., 2008). Based on this previous work, events sharing a common exemplar were predicted to be associated with the most highly similar patterns of activity in ventral visual cortex, with these patterns becoming increasingly dissimilar as the events become more distinct. However, older adults were predicted to exhibit reduced sensitivity to variations in stimulus content in ventral visual cortex, possibly displaying reduced similarity between highly related events, and increased similarity between distinct events (Carp et al., 2011).

To assess the degree to which encoding-related activity was reinstated during retrieval, the neural pattern similarity between corresponding encoding and retrieval events (within-event encoding-retrieval similarity [ERS]) was computed, and compared to the similarity between non-corresponding encoding and retrieval events (between-event ERS). Greater similarity between corresponding, relative to non-corresponding, events is thought to be indicative of reinstatement of encoding-related activity during retrieval (e.g., Staresina et al., 2012). To investigate the specificity of cortical reinstatement, separate measures were created to assess the similarity between i) non-corresponding events that shared the same exemplar as the target event, and therefore common perceptual and conceptual information, and ii) non-corresponding events that contained an exemplar from the opposite stimulus category, and therefore shared minimal perceptual or conceptual information with the target event. This enabled an assessment of whether individuals retrieved event-specific details from encoding to make recognition decisions, or more general conceptual details. Each of these measures was computed separately for intact and recombined pairs to determine the effects of retrieval cue properties on reinstatement effects.

This analysis was focused within four anatomical regions of interest, including the ventral visual cortex, angular gyrus, inferior prefrontal cortex, and hippocampus. These regions were selected a priori due to their involvement in both episodic encoding and retrieval, and because they have previously been identified as sensitive to event-specific or category-level reinstatement effects (e.g., Kuhl & Chun, 2012, Bonnici, Richter, Yazar, & Simons, in press). Younger adults were predicted to exhibit evidence for event-specific reinstatement of encoding-related activity during both hits and correct rejections, with greater within- relative to between-event ERS, even when comparison events shared the same exemplar, consistent with the retrieval of the original paired associate to support recognition decisions. In contrast, older adults are less likely to use such a recollection-based retrieval strategy, and therefore are less likely to exhibit event-specific reinstatement effects. This may be accompanied by retrieval of more general event information, resulting in less-specific, category-level reinstatement effects, with greater within- relative to between- event ERS only when comparison events are highly distinct (e.g., contain opposite category information). Alternatively, evidence for reinstatement of encoding-related activity may be absent among older adults altogether, suggesting a failure to engage recollection-based retrieval strategies with age. The degree to which older adults exhibit reinstatement effects may vary according to the retrieval cue. In particular, reinstatement may be more likely during trials comprising intact pairs relative to recombined pairs if these provide greater support for guiding retrieval of the original association, but not if they support performance by simply facilitating the use of familiarity to make accurate responses.

Method

Participants

Twenty younger adults aged 21-30 (mean = 24.9 years) and 20 older adults aged 63-79 (mean = 71.4 years) were included in the present analysis. Participants in both groups were recruited from the MRC Cognition and Brain Sciences Unit volunteer panel as well as the surrounding Cambridge community and received £20 for participating in the study. All participants were healthy, right-handed, had normal or corrected-to-normal vision and hearing, and were free from any psychiatric or neurological conditions. Two additional older adults were tested but excluded from the analysis, one due to falling asleep in the scanner and failure to complete the session, and another due to performance below the normal range on the Montreal Cognitive Assessment (MoCA; cut off >= 26). All remaining older adults performed within the normal range on the MoCA (*M* = 27.8). Older and younger adults did not differ with respect to years of formal education (*t*(38) = 1.60, *p* = .118), and older adults performed higher on the Shipley Institute of Living Scale (*t*(38) = 3.55, *p* < .001). Informed consent was obtained in accordance with the Cambridge Psychology Research Ethics Committee.

Materials

Experimental stimuli consisted of 192 word-picture pairs comprised of trial-unique adjectives paired with one of eight coloured pictures. Four of these pictures were of objects, and of these two were of living things and two were of non-living, inanimate objects, and the remaining four were of scenes, two depicting indoor settings and two outdoor settings (Figure 4). All adjective-picture pairings were fixed across participants, and were created to ensure that the picture could plausibly be imagined in accordance with the adjective. Word-picture pairs were randomly assigned to one of three 64-item study lists, with the constraint that each list contained eight pairs corresponding to each of the eight pictures. Half of the study items were subsequently presented as intact pairs during the test phase, and the other half were presented as recombined pairs. The assignment of pairs as intact or recombined was counterbalanced across participants. All recombined pairs comprised a studied word and a picture taken from the opposite category to ensure that neural activity patterns corresponding to the target image and the cue image were maximally distinct. During the test phase, each associated picture was also replaced with a common noun denoting each image (e.g., TEAPOT, BEDROOM) to avoid an identical perceptual match between encoding and retrieval. The presentation of word-picture pairs during each study and test block was pseudo-randomized for each participant, with the constraint that no more than four images from the same category appeared in sequence, and that each image was not presented more than twice in a row. The test phase included the additional constraint that no more than four intact or recombined pairs occurred in sequence. Stimuli were presented using the Cogent software package implemented in MATLAB (Mathworks, Inc., USA).

Procedure

The experimental paradigm is depicted in Figure 1. Each study block comprised 64 trials in which participants were presented with a word-picture pair and were instructed to imagine the picture in accordance with the adjective, and to indicate whether they had been successful in doing so with a button press response (1 = successful, 2 = unsuccessful). Each study block was followed by a one-minute retention interval during which participants were asked to covertly count backwards from a random number presented on the screen. The test phase commenced immediately afterwards. During each test block trial, participants were presented with a studied adjective and a word corresponding to one of the eight pictures and indicated with a single button press whether the pairing was studied or novel (1 = old, 2 = new). Both study and test trials lasted for a fixed duration of 5000 ms, with an inter-trial interval of 1000 ms. Participants completed three alternating study-test blocks in this fashion, with a one-minute break between each cycle during which they were instructed to close their eyes and rest.

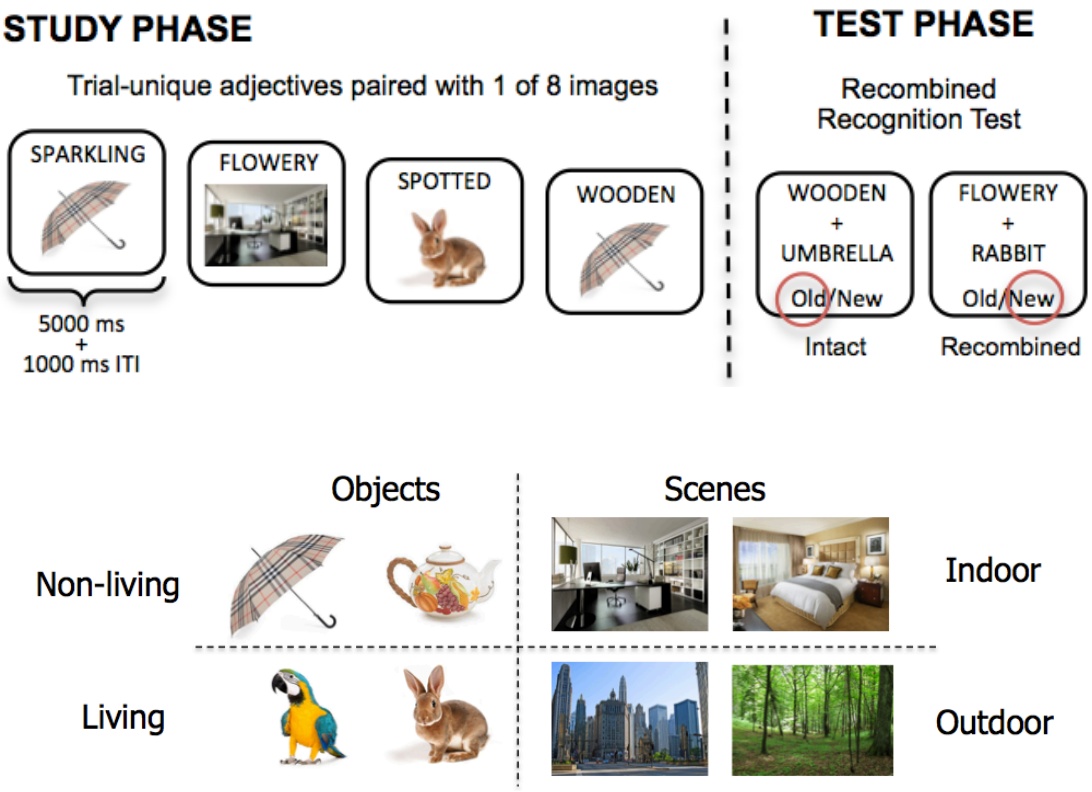

Figure 1. Schematic depicting experimental paradigm (top). Participants studied trial-unique adjectives paired with one of eight images (bottom). At test, participants were presented with studied (intact) and non-studied (recombined) pairs and made an old/new judgment for each. Correct responses are circled. Pictures were replaced with word labels during the test phase to minimise perceptual overlap between study and test.

fMRI Data Acquisition and Pre-processing

Scanning was performed using a 3-T Siemens Trio MRI system with a 32-channel head coil. Functional data was acquired using a descending Blood-Oxygenation-Level-Dependent (BOLD)-weighted echo-planar imaging (EPI) pulse sequence (repetition time (TR) =2000 ms, echo time (TE) = 30 ms, flip angle = 78). Each EPI volume consisted of 32 axial slices (3mm thick, 0.75 mm gap, 3 x 3 mm in-plane resolution) covering the whole brain. For each of the six sessions (3 study and 3 test blocks) 210 volumes were acquired. The first five volumes of each session were discarded to allow for magnetic field stabilization. A high-resolution (1 x 1 x 1 mm) T1-weighted anatomical image was also acquired at the beginning of the scanning session using a 3D magnetization-prepared rapid acquisition gradient echo (MP-RAGE) pulse sequence.

Data pre-processing and univariate analysis was conducted using SPM12 (http://www.fil.ion.ucl.ac.uk/spm/) and batched using “automatic analysis” software (MRC CBU, https://github.com/rhodricusack/automaticanalysis/). Preprocessing of image volumes included spatial realignment to correct for movement, followed by slice-timing correction, using the first acquired slice in each session as a reference. Functional volumes were then coregistered to structural images, and spatial normalisation of images into MNI stereotactic space was performed using high-dimensional DARTEL image registration (Ashburner, 2007).

Univariate Analysis

For univariate analyses, EPI images were additionally smoothed with an isotropic 8-mm full-width-at half-maximum (FWHM) Gaussian kernel. Neural activity was modeled by delta functions at stimulus onset for each event of interest and convolved with a canonical hemodynamic response function (HRF). The resulting timecourses were downsampled at the midpoint of each scan to form regressors in the General Linear Model (GLM). Two models were created, one to explore stimulus category effects during encoding, and the other to explore memory success effects during retrieval. The study model contained two regressors of interest representing the two stimulus categories, objects and scenes, as well as 6 additional regressors of no interest for each session representing the movement parameters estimated during spatial alignment (3 rigid-body translations, 3 rotations). All study trials were included as events of interest, irrespective of subsequent memory performance for the pair presented on each trial. The test model contained two regressors of interest, in this case representing the two types of successful retrieval events: hits and correct rejections, collapsed across stimulus category. All remaining trials (misses, false alarms, no response) formed a third regressor of no interest, and 6 additional regressors representing movement parameters were additionally included. Note that subsequent memory and retrieval success effects, which compare activity associated with hits as compared to misses during encoding or retrieval, respectively, could not be examined in the current experiment due to an insufficient number of forgotten trials in the younger group.

Voxel-wise parameter estimates for each regressor were obtained by maximum-likelihood estimation, using a temporal high pass filter (cut-off 128 s) to remove low-frequency drifts. First-level contrasts of the parameter estimates for each participant were then entered into a second-level analysis, with participants treated as a random-effect. For study blocks, contrasts corresponded to stimulus category (Objects versus Scenes), whereas for the test blocks, contrasts corresponded to memory type (Hits [H] versus Correct Rejections [CR]). A 2 x 2 mixed ANOVA was conducted for each block type to examine both main effects as well as condition-by-group interactions. For the study data, the ANOVA contained the factors of Category (object, scene) and Age (young, old), whereas for test data the ANOVA contained the factors of Memory Type (H, CR) and Age (young, old). All effects were thresholded at a significance level of $p < .05$ using a family wise error (FWE) correction for multiple comparisons across the whole brain. As an additional control to assess whether age differences in regional BOLD activity might be present in the anatomically defined regions of interest (ROIs) used for the multivariate analyses (described below), the contrasts described above were repeated in each of the four regions (ventral visual cortex, hippocampus, angular gyrus, and inferior prefrontal cortex) using a more lenient small volume correction (SVC). Note that these ROIs were not selected based on the whole brain results, but were chosen a priori based on existing results in the literature.

Multivariate Pattern Similarity Analysis

Pattern similarity analyses were applied to the preprocessed but unsmoothed fMRI data (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Jimura & Poldrack, 2012). Data from all 6 scanning sessions were modeled in a single GLM containing a separate regressor for each trial. Six movement parameters and a mean-term were included for each session as regressors of no interest. This procedure yielded 384 beta images, 192 corresponding to study trials and 192 corresponding to test trials. The multivariate patterns used in the subsequent analysis were obtained by extracting raw beta values from each voxel in each anatomical region of interest. These regions included a ventral visual cortex ROI, comprised of inferior occipital lobe, parahippocampal gyrus, fusiform gyrus, and lingual gyrus (Wimber et al., 2015), an inferior prefrontal cortex ROI, comprised of pars orbitalis and pars triangularis (Badre & Wagner, 2007), an angular gyrus ROI, and a hippocampal ROI. All ROIs were bilateral and created using the automated anatomical labeling (AAL) atlas implemented in the WFU pickatlas software (http://fmri.wfubmc.edu/software/PickAtlas). This resulted in two trial x voxel matrices for each ROI representing the activity patterns across individual voxels during each trial, separately for study and test. Any voxels that contained NaN values were excluded from all participants.

Feature selection was then performed to select voxels within each ROI that best differentiated between the 8 images during the study phase. This was done by running a GLM containing 8 regressors, representing each of the 8 images, in every voxel of each ROI, producing an *F*-contrast testing for differences between the 8 means for each voxel. As the ROIs were not equally sensitive to the different exemplars, a significance threshold was selected that yielded a minimum of 50 voxels in each ROI across participants on average. This threshold was $p < 0.30$, and yielded an average of 1255 voxels in ventral visual cortex, 160 voxels in angular gyrus, 280 voxels in inferior prefrontal cortex, and 77 voxels in the hippocampus. Due to variability in the number of voxels that fell below this threshold for each participant, this group average was used to equate the number of voxels selected for each participant in each ROI. To ensure that voxel selection remained unbiased, a leave-two-out procedure was applied wherein the data from all participants, except one younger and one older adult, were used to select voxels for the two left out participants. On each iteration, voxels were sorted in ascending order based on their corresponding *p*-values, and the lowest 1255, 160, 280, and 77 voxels were chosen for each of the four ROIs, respectively. This procedure was repeated 20 times until selection for all participants was complete.

For the analysis of stimulus-specific differentiation during encoding, pairwise Pearson correlation was computed between all encoding trials, irrespective of subsequent memory accuracy, producing a 192 x 192 correlation matrix for each subject and each ROI. These were then used to compute the average pairwise correlation across trials corresponding to each of the four event types based on the image exemplar presented on each trial. This produced four measures of study phase similarity, including *same-exemplar similarity, same-subcategory similarity, same-category similarity, and different-category similarity.*

To assess the reinstatement of encoding-related activity patterns during retrieval, pairwise correlations were computed between all study and test trials that received an accurate recognition decision, producing a measure of encoding-retrieval similarity (ERS) for all possible pairwise comparisons. This was computed separately for hits and correct rejections, yielding two separate matrices of pairwise study-test correlations (Figure 2). A measure of *within-event similarity* was created by computing the mean pairwise correlation between study and test trials corresponding to the same event (e.g., encoding and retrieval of 'Artistic Parrot'). Two measures of between-event similarity were created to measure ERS between study and test trials of non-corresponding events. The first represented the mean pairwise correlation between encoding and retrieval of non-corresponding events that shared the same exemplar (e.g., encoding of 'Sparkling Umbrella' and retrieval of 'Golden Umbrella'), henceforth *between-event ERS, Same Exemplar (SE)*. The second measure of between-event ERS represented the mean pairwise correlation between encoding and retrieval of non-corresponding events that contained exemplars from the opposite category (e.g., encoding of 'Sparkling Umbrella' and retrieval of 'Flowery Office'), henceforth *between-event ERS, Different Category (DC)*. This enabled a comparison of within-event ERS and between-event ERS when comparison events were both perceptually and conceptually similar to the target event (SE), relative to when comparison events were both perceptually and conceptually distinct from the target event (DC). Each of these ERS scores was computed separately for hits and correct rejections and for each region of interest. All correlations were Fisher z-transformed before any averaging or statistical analyses were performed.

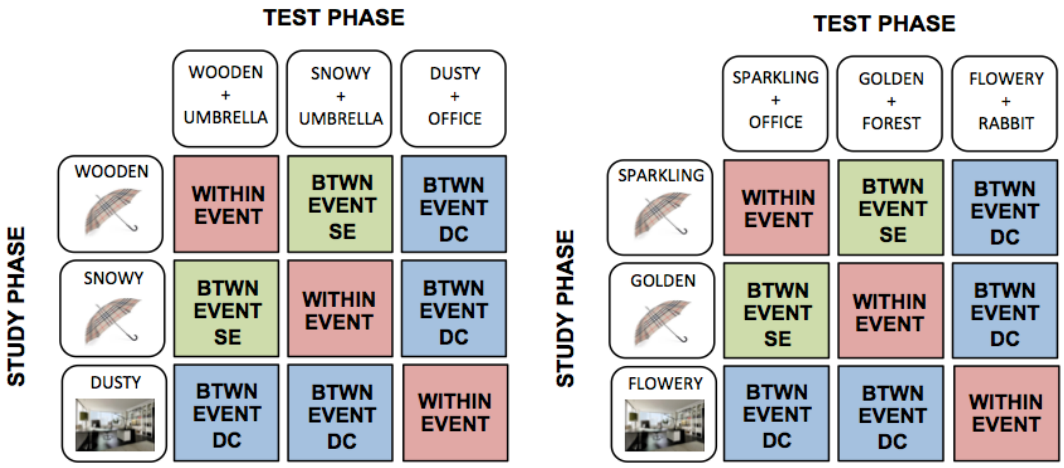

Figure 2. Schematic depicting encoding-retrieval similarity matrix for hits (left) and correct rejections (right). Within-event similarity represents the similarity between corresponding study and test trials. Between-event (SE) represents the similarity between non-corresponding study and test trials sharing the same exemplar. Between-event (DC) represents the similarity between non-corresponding study and test trials with associates that belonged to the opposite stimulus category.

Results

Behavioural Results

Recognition memory was calculated as the proportion of hits to intact pairs corrected by the proportion of false alarms to recombined pairs. Independent samples *t*-tests revealed that memory performance was significantly impaired in older adults relative to younger adults ($t(38) = 6.35$, $p < .001$, $d = 2.06$), and that this was driven by both a lower hit rate ($t(38) = 4.67$, $p < .001$, $d = 1.52$) and an increased false alarm rate ($t(38) = 5.75$, $p < .001$, $d = 1.87$). To determine whether age differences in memory performance could be explained by age differences in subjective imagery success during encoding, as younger adults reported imagining a greater proportion of events relative to older adults ($t(38) = 3.92$, $p < .001$, $d = 1.27$), imagery success was included as a covariate in the model. Although imagery success was a significant predictor of performance ($F(1,37) = 16.64$, $p < .001$, $\eta_p^2 = 0.310$), it did not account for the effects of age, which remained significant ($F(1,37) = 17.42$, $p < .001$, $\eta_p^2 = 0.320$).

fMRI Univariate Results

Regions exhibiting sensitivity to stimulus category during encoding are presented in Table 1 and depicted in Figure 3 (left). Areas exhibiting increased activity during object trials as compared to scene trials included the right inferior and middle temporal cortex, bilateral fusiform gyrus, left inferior occipital cortex, and right cuneus. Regions exhibiting the opposite effect, with greater activity during scene trials, included the bilateral fusiform gyrus, right calcarine sulcus, right precuneus, and middle cingulate cortex. No significant clusters were identified for the main effect of Age or the Category x Age interaction.

When this analysis was restricted to voxels within the ventral visual cortex ROI, many of the same regions were identified in the category contrast. Regions exhibiting greater activity during object trials relative to scene trials included bilateral inferior occipital gyrus, left lingual gyrus, right parahippocampal gyrus, and bilateral fusiform gyrus. Regions exhibiting greater activity during scene trials relative to object trials included bilateral fusiform gyrus and left lingual gyrus. As in the whole brain analysis, no suprathreshold clusters were detected in which younger adults exhibited greater activity than older adults (all $p > .185$) or vice versa (all $p > .13$). However, two clusters were identified for the Category x Age interaction in the right fusiform gyrus and left lingual gyrus, which were driven by significantly greater activity in older adults relative to younger adults during object trials. The opposite interaction (young > old) did not reveal any suprathreshold clusters (all $p > .270$ with FWE correction).

Table 1: Peak voxels showing a main effect of stimulus category during encoding, p < .05 FWE corrected. Voxel numbers reported are for entire cluster.

Region	Voxels	MNI Coordinates (x, y, z)			Peak *t* value
Objects > Scenes					
R inferior temporal gyrus	1242	48	-72	-6	14.24
R middle temporal gyrus		51	-60	3	12.71
R fusiform gyrus		42	-48	-18	10.39
L inferior occipital gyrus	1302	-42	-81	-9	13.27
L inferior occipital gyrus		-48	-78	-3	12.12
L fusiform gyrus		-42	-51	-18	10.91
R cuneus	325	3	-81	-9	10.49
L calcarine sulcus		-18	-78	6	6.69
L lingual gyrus		-9	-66	-3	6.60
Scenes > Objects					
L fusiform gyrus	4346	-27	-51	-9	22.45
R fusiform gyrus		-27	-54	-9	19.43
R calcarine sulcus		21	-57	15	18.90
R precuneus	82	6	-42	45	7.86
L middle cingulate cortex		-6	-39	42	7.41

Next, regions associated with the two different types of successful memory retrieval were identified by contrasting correct ‘old’ responses to intact pairs (Hits) and correct ‘new’ responses to recombined pairs (CRs), irrespective of the stimulus category on each trial (Table 2; Figure 3, right). Regions exhibiting greater activity during hits relative to correct rejections included bilateral parahippocampal cortex, left hippocampus, left superior medial frontal gyrus, left lingual gyrus, left inferior parietal cortex, left angular gyrus, right cuneus, right middle occipital cortex, left middle cingulate cortex, and left caudate. The opposite contrast identifying regions exhibiting greater activity for correct rejections relative to hits yielded only one suprathreshold cluster in the right lingual gyrus. No significant clusters were identified for the main effect of Age, nor the Memory Type x Age interaction.

This analysis was then conducted in each of the four ROIs. Consistent with the whole brain effects, greater activity for hits relative to correct rejections was observed in left angular gyrus, left inferior frontal gyrus, bilateral hippocampus, and ventral visual cortex. The opposite contrast did not reveal any suprathreshold clusters in the angular gyrus, hippocampus, or inferior frontal gyrus, but did reveal one cluster in the ventral visual cortex, localised in the right lingual gyrus. The main effect of age yielded one suprathreshold cluster in ventral visual cortex, with older adults exhibiting greater activity in the left inferior occipital gyrus relative to younger adults. No significant clusters were identified for the Memory Type x Age interaction across any regions of interest.

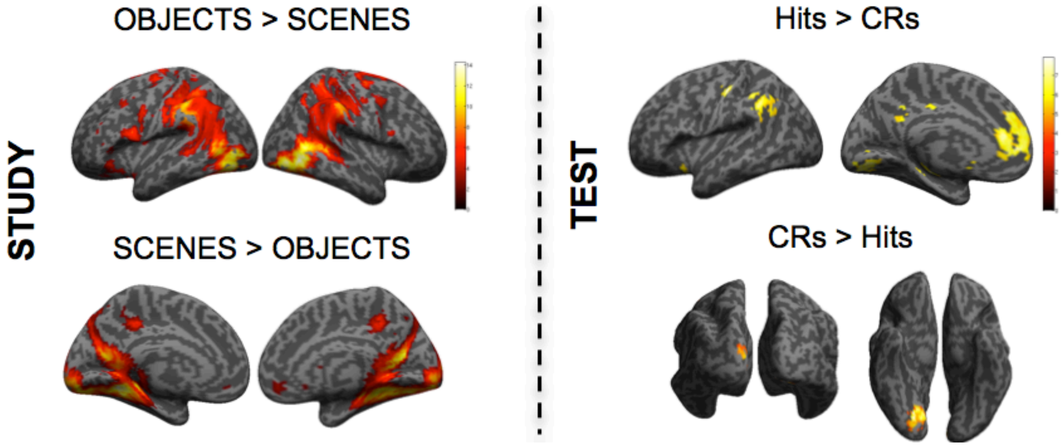

Figure 3. Results of the whole brain univariate contrasts for stimulus category during the study phase (left) and successful retrieval during the test phase (right), common to older and younger adults. All effects were thresholded at a significance level of p < .05 with FWE correction for multiple comparisons and a 5-voxel extent threshold.

Table 2: Peak voxels showing a main effect of successful memory during retrieval, p < .05 FWE corrected. Voxel numbers reported are for entire cluster.

Region	**Voxels**	**MNI Coordinates (x, y, z)**			**Peak *t* value**
Hits > CRs					
L parahippocampal gyrus	33	-27	-30	-12	7.96
L Hippocampus		-30	-18	-18	5.44
L superior medial frontal gyrus	442	-6	51	6	7.65
L superior medial frontal gyrus		-6	57	15	7.27
L anterior cingulate cortex		-6	39	12	7.26
L lingual gyrus	120	-12	-78	-9	7.51
L inferior parietal cortex	133	-54	-45	39	7.37
L angular gyrus		-54	-57	27	6.07
L inferior parietal cortex		-48	-57	45	5.81
R cuneus	63	12	-93	21	7.24
R middle occipital gyrus	28	42	-81	24	6.82
R parahippocampal gyrus	29	27	-18	-18	6.76
L middle cingulate cortex	53	0	-18	39	6.33
R middle cingulate cortex		9	-24	39	5.78
L caudate	10	-6	9	-3	6.30
CRs > Hits					
R lingual gyrus	39	18	-75	-9	7.11

In summary, age differences in regional BOLD activity for category-selective effects or retrieval success effects were negligible across both whole brain and ROI analyses. This observation suggests that any age differences in multivariate pattern similarity measures are unlikely to be driven by age differences in univariate signal strength across regions.

fMRI Multivariate Pattern Similarity Results

Age Differences in Stimulus-Specific Differentiation during Encoding

To assess whether activity patterns were sensitive to stimulus relatedness during encoding, the similarity between activity patterns associated with encoding events was compared across the range from highly related (e.g., those sharing the same exemplar) to highly distinct (e.g., those containing images from different categories). This produced four different similarity scores: *Same Exemplar Similarity, Same Subcategory Similarity, Same Category Similarity, and Different Category Similarity* (Figure 4). To assess the effect of event-relatedness on pattern similarity in ventral visual cortex across groups, a 4 x 2 ANOVA was conducted with Level as a within-subjects factor (SE, SS, SC, DC) and Age (young, old) as a between-subjects factor.

The ANOVA revealed a main effect of Level ($F(3, 114) = 156.91, p < 0.001, \eta_p^2 = 0.805$) and a Level x Age interaction ($F(3, 114) = 46.47, p < 0.001, \eta_p^2 = 0.550$), but no main effect of Age ($F < 1$). Follow-up *t*-tests at each level of event similarity revealed that older adults exhibited lower levels of Same Exemplar Similarity ($t(38) = 2.26, p < .05, d = 0.73$) and increased levels of Different Category Similarity ($t(38) = 4.37, p < .001, d = 1.42$) relative to younger adults. Older adults also displayed numerically lower pattern similarity for events belonging to the Same Subcategory and the Same Category, but these differences did not reach significance (SS: $t(38) = 1.89, p = .067, d = 0.61$; SC: $t(38) = 1.67, p = .10, d = 0.54$).

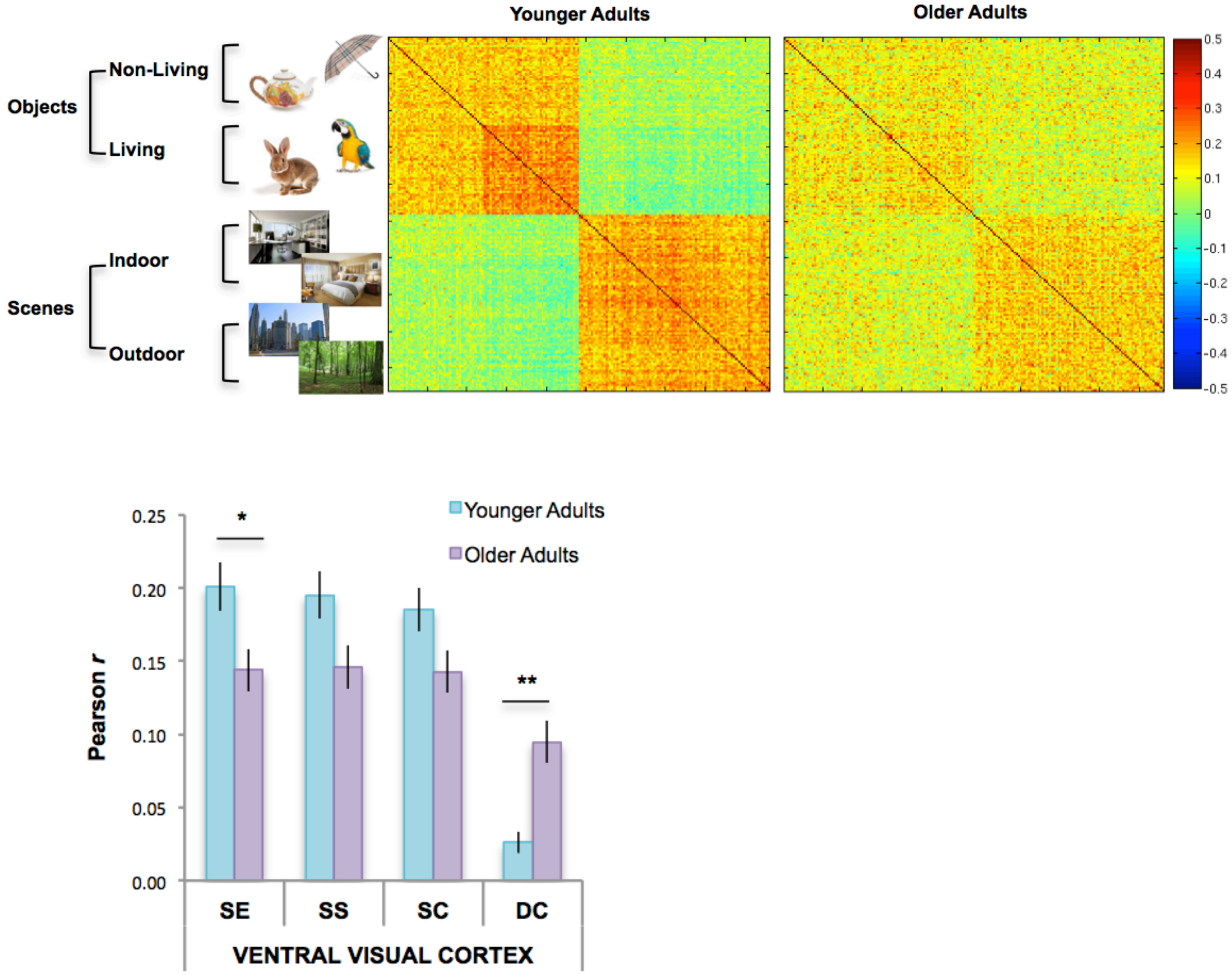

*Figure 4. A. Hierarchical structure of visual stimuli (left) and corresponding representational similarity matrices in ventral visual cortex for younger and older adults (right). B. Mean pairwise correlations between events of each type in older and younger adults; SE = Same Exemplar; SS = Same Subcategory; SC = Same Category; DC = Different Category. Error bars represent standard error of the mean; * = p < .05; ** = p < .01.*

Relationship between Representational Distinctiveness and Memory Performance

To examine whether the differentiation of stimulus representations in ventral visual cortex was related to subsequent memory performance, a measure of representational distinctiveness was computed by subtracting *Different Category*

Similarity from *Same Category Similarity.* This yielded a difference score representing the degree to which activity patterns in this region differentiated between stimulus categories (e.g., Carp et al., 2011). As predicted, this score was significantly larger in younger adults ($M_{\text{diff}} = 0.19$) as compared to older adults ($M_{\text{diff}} = 0.05$; $t(38) = 6.91$, $p < .001$, $d = 2.24$). When this score was correlated with correct recognition performance in each age group, this revealed a significant relationship between neural distinctiveness and corrected recognition in younger adults ($r = .458$, $p < .05$), which was not present in older adults ($r = .062$, $p = .795$; see Figure 5). However, these two relationships did not differ ($z = 1.26$, $p = .21$), making it difficult to rule out the possibility that this relationship might also be observed in among older adults if there was greater variability in distinctiveness scores.

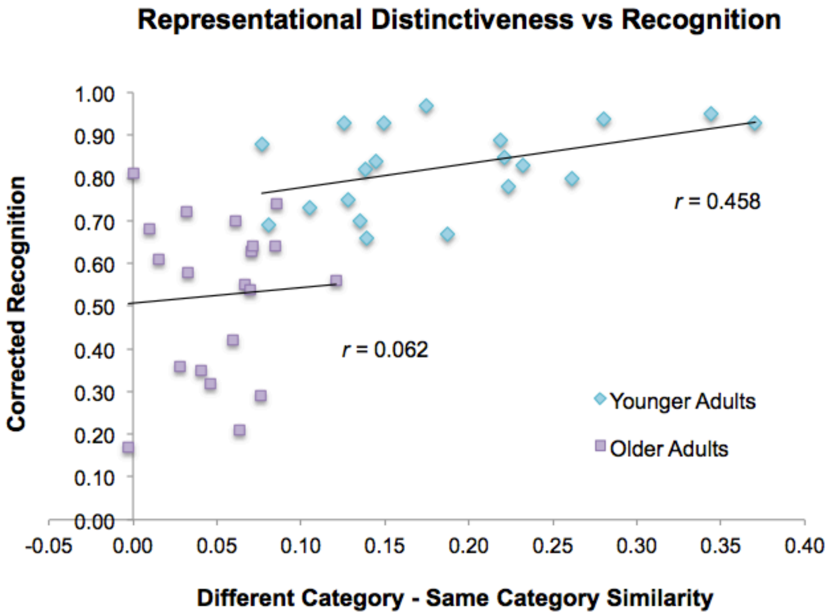

Figure 5. Representational Distinctiveness in Ventral Visual Cortex (VVC) during encoding, calculated as Different Category Similarity – Same Category Similarity, plotted against corrected recognition memory performance (Hits-False Alarms) in older and younger adults. Higher representational distinctiveness was positively correlated with corrected recognition in younger adults, whereas this relationship was not present in older adults.

Event-Specific Reinstatement during Retrieval

Next, I explored the degree to which older and younger adults exhibited event-specific reinstatement of encoding-related activity during retrieval, and whether this differed according to whether the test cue was an intact or recombined pair. To assess this, two measures of encoding-retrieval similarity (ERS) were computed: i) *within-event ERS*, the average similarity between the encoding and retrieval patterns of corresponding study and test trials (e.g., encoding and retrieval of ‘Sparkling Umbrella’), and ii) *between-event ERS (SE)*, or the average similarity between encoding and retrieval patterns of non-corresponding study and test trials that shared the same exemplar (e.g., encoding of ‘Sparkling Umbrella’ and retrieval of ‘Golden Umbrella’). If within-event ERS is greater than between-event ERS (SE), this is evidence for reinstatement of event-specific encoding activity during retrieval, which cannot be driven by general exemplar or category level effects (see Figure 4). Within-event ERS and between-event ERS were computed separately for each trial type, hits and correct rejections, and these scores were submitted to a mixed ANOVA with Event Type (within, between) as a within-subjects factor and Age (young, old) as a between-subjects factor in each ROI. The results are depicted in Figure 6.

With respect to Hits, a trend towards an Event Type x Age interaction was identified in ANG ($F(1,38) = 3.24, p = .08, \eta_p^2 = .079$), an effect that did not approach significance in the remaining regions (all $p > .20$). Follow-up paired t-tests comparing within-event ERS and between-event ERS (SE) in ANG for each age group revealed greater within- relative to between-event ERS in younger adults ($t(19) = 2.38, p < .05, d = 1.09$), providing evidence for event-specific reinstatement, whereas the same effect was not exhibited by older adults ($t < 1$).

With respect to CRs, an Event Type x Age interaction was observed in ANG ($F(1,38) = 7.94$, $p < .01$, $\eta_p^2 = .173$), and INF PFC ($F(1,38) = 5.96$, $p < .05$, $\eta_p^2 = .136$), and a trend was evident in VVC ($F(1,38) = 3.44$, $p = .072$, $\eta_p^2 = .083$). A main effect of Age was also observed in VVC ($F(1,38) = 4.11$, $p < .05$, $\eta_p^2 = .098$), with older adults exhibiting higher levels of ERS overall. Follow-up paired t-tests comparing within-event ERS and between-event ERS in each region revealed evidence for event-specific reinstatement in younger adults in ANG ($t(19) = 2.33$, $p < .05$, $d = 1.07$) and INF PFC ($t(19) = 2.60$, $p < .05$, $d = 1.19$), but these differences were not significant in older adults (all $p > .09$). In VVC, this difference was not significant in either age group (all $p > .120$).

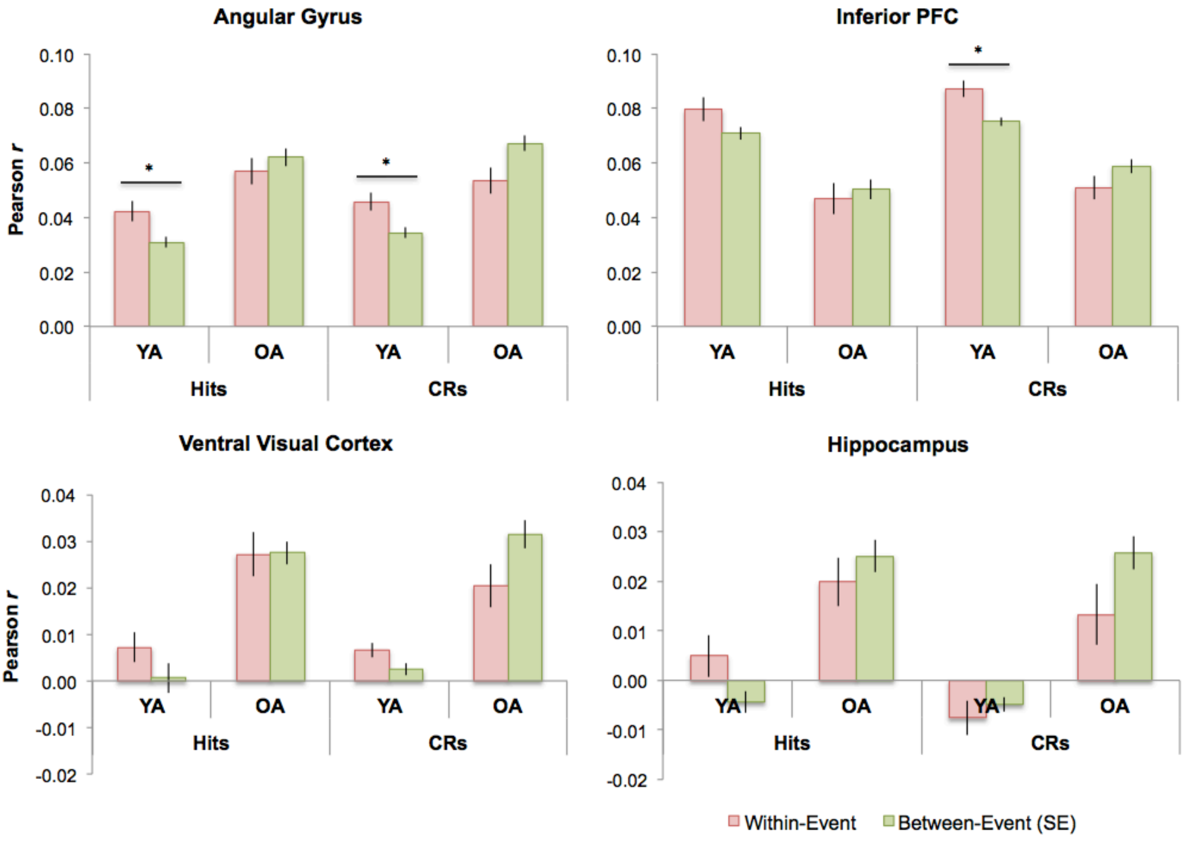

*Figure 6. Mean pairwise correlations for within-event similarity and between-event similarity (Same Exemplar) in each region of interest. Event-specific reinstatement = within-event similarity > between-event similarity (SE); Error bars represent standard error of the mean; * = p < .05.*

Category-Level Reinstatement during Retrieval

As older adults did not exhibit evidence for event-specific reinstatement, I next assessed whether older adults instead exhibited less specific, category-level reinstatement during retrieval. This would be consistent with the proposal that older adults are more likely to retrieve general conceptual details from the study event to support recognition, rather than highly specific event details. For example, older adults may recall that the adjective ‘Sparkling’ was paired with an object, but not be able to bring to mind details of the specific ‘Sparkling-Umbrella’ association. To answer this question, a similar analysis was conducted as that described in the previous section, again comparing within-event ERS to between-event ERS for both hits and correct rejections. This time, however, the measure of between-event ERS reflected the mean pairwise correlation between only those non-corresponding study and test trials that contained an exemplar from the opposite category (e.g., encoding of ‘Sparkling Umbrella’ and retrieval of ‘Flowery Office; see Figure 2). These ERS scores were calculated for both hits and correct rejections, and submitted to an Event Type (within, between) x Age ANOVA in each ROI. The results are depicted in Figure 7.

With respect to Hits, a main effect of Event Type ($F(1,38) = 7.10, p < .05, \eta_p^2 = .157$), and Age ($F(1,38) = 5.80, p < .05, \eta_p^2 = .132$) emerged in VVC, as well as a trend towards an Event Type x Age interaction ($F(1,38) = 3.07, p = .08, \eta_p^2 = .075$). In ANG, there was a main effect of Event Type ($F(1,38) = 4.89, p < .05, \eta_p^2 = .114$), which was qualified by an Event Type x Age interaction ($F(1,38) = 4.05, p < .05, \eta_p^2 = .096$). Follow-up paired *t*-tests in each region revealed evidence for category-level reinstatement (within-event ERS > between-event ERS, DC) in younger adults in VVC ($t(19) = 4.07, p < .001, d = 1.87$) as well as ANG ($t(19) = 3.46, p < .005$, 1.59), however these effects were not observed in older adults (all $t < 1$), suggesting the main effect of Event Type was driven by younger adults in both regions.

With respect to CRs, an Event Type x Age interaction was present in VVC ($F(1,38) = 4.48, p < .05, \eta_p^2 = .105$) and ANG ($F(1,38) = 11.02, p < .005, \eta_p^2 = .225$), with a similar trend in INF PFC ($F(1,38) = 3.39, p = .07, \eta_p^2 = .082$). Follow-up paired *t*-tests in these regions revealed greater within-event relative to between-event ERS (DC) in younger adults in ANG ($t(19) = 2.66, p < .05, d = 1.22$) and INF PFC ($t(19) = 2.43, p < .05, d = 1.11$). In contrast, older adults exhibited the opposite pattern in ANG, with greater between-event ERS relative to within-event ERS ($t(19) = 2.18, p < .05, d = 1.0$). A similar pattern was observed in VVC, with younger adults exhibiting a tendency towards within-event ERS > between-event ERS and older adults exhibiting the opposite pattern, but these effects did not reach significance (all $p > .09$). Older adults did not exhibit reinstatement effects in INF PFC ($t < 1$). These results suggest that the absence of event-specific reinstatement effects among older adults was not due to reinstatement of less specific, category-level information during retrieval, but perhaps instead due to the adoption of a different retrieval strategy, a point addressed further in the discussion.

Relationship between Reinstatement Specificity and Memory Performance

To examine whether the observed evidence for event-specific and category-level reinstatement was related to subsequent memory performance, a reinstatement specificity score was calculated by subtracting between-event ERS from within-event ERS in each instance where reinstatement effects were observed (e.g., within-event ERS > between-event ERS, or vice versa). These reinstatement specificity scores

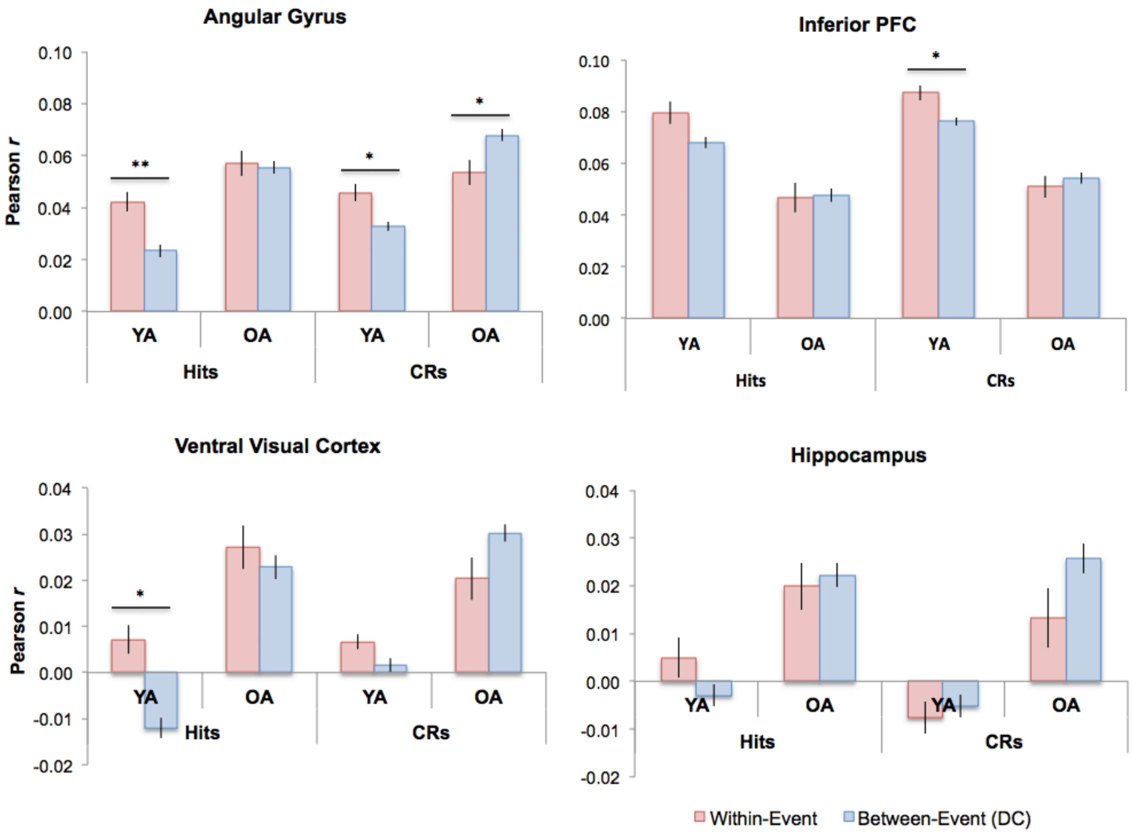

*Figure 7. Mean pairwise correlations for within-event similarity and between-event similarity (Different Category) in each region of interest. Category-level reinstatement = within-event similarity > between-event similarity (DC); Error bars represent standard error of the mean; * = p < .05; ** = p < .01.*

were computed separately for event-specific reinstatement and for category-level reinstatement when both effects were observed. For younger adults, this produced an event-specific and category-level reinstatement specificity score in ANG and INF PFC for correct rejections and in ANG for hits, as well as a category-level reinstatement specificity score for hits in VVC. In older adults, this yielded a category level reinstatement specificity score for CRs in ANG. These scores were then correlated with hit rate or correct rejection rate, according to the trial type during which they were observed.

In older adults, a significant negative relationship was observed between category-level reinstatement specificity in ANG and correct rejection rate (*r* = -.444, *p* < .05), indicating that more negative reinstatement values were associated with an increased likelihood of correct rejections (or conversely, that more positive values were associated with false alarms; see Figure 8). Younger adults exhibited a non-significant relationship in the other direction (*r* = .300, *p* = .198), indicating that greater reinstatement specificity was associated with a higher correct rejection rate, and these two correlations were significantly different from one another (*z* = 2.29, *p* < .05). Among younger adults, none of the remaining relationship between reinstatement specificity and hit rate or CR rate reached significance (all *r* < .38, all *p* > .103).

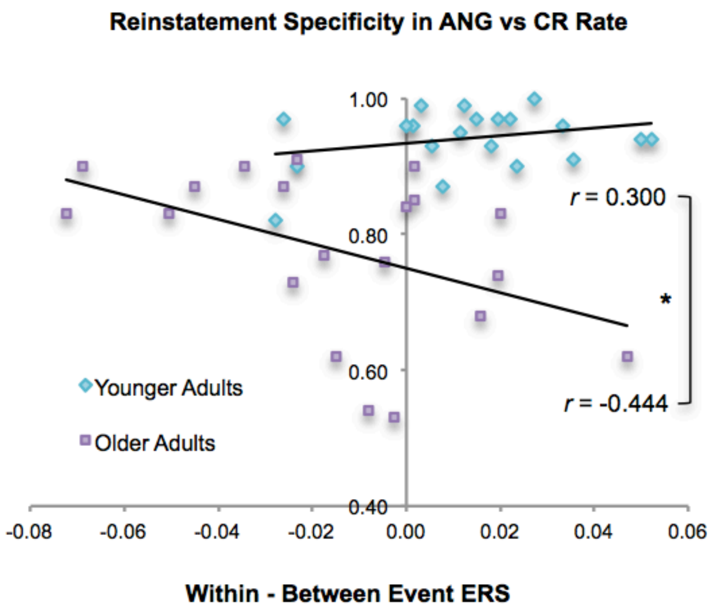

Figure 8. Reinstatement specificity in Angular Gyrus (ANG) during Correct Rejections (CR), calculated as Within-Event Similarity – Between-Event Similarity (DC) plotted against CR rate in older and younger adults. Higher reinstatement specificity was positively correlated with CR rate in younger adults, but negatively correlated with CR rate in older adults.

Relationship Between Representational Distinctiveness and Reinstatement Specificity

Previous work has suggested that age-related reductions in reinstatement specificity during retrieval can be driven by dedifferentiation of stimulus representations during encoding (Johnson et al., 2015; but see St-Laurent et al., 2014). To investigate this possibility, the present measure of representational distinctiveness in VVC during encoding (Different Category Similarity – Same Category Similarity) was correlated with reinstatement specificity (within-event ERS – between event ERS) during hits or correct rejections across groups (see Figure 9). Among older adults, representational distinctiveness was positively related with event-specific (r = .457, $p < .05$) and category-level (r = .451, $p < .05$) reinstatement specificity in ANG during hits, as well as with category-level reinstatement specificity in INF PFC during hits (r = .446, $p < .05$). These relationships suggest that dedifferentiation during encoding may contribute to the absence of evidence for reinstatement effects during hits among older adults. In contrast, these relationships were not observed during correct rejections for event-specific reinstatement in ANG (r = .044, p = 0.854; difference: z = 1.70, p = .08), category-level reinstatement in ANG (r = .005, p = 0.984; difference: z = 1.77, p = .07), or category-level reinstatement in INF PFC (r = -.266, p = 0.256; difference: z = 1.97, $p < .05$), suggesting that representational distinctiveness at encoding is less likely to account for the absence of reinstatement effects during correct rejections among older adults.

Note that younger adults did not exhibit a relationship between representational distinctiveness and reinstatement specificity during hits or correct rejections across regions (all $r < .11$, all $p > .30$). This may have been due to the relatively high level of representational distinctiveness among younger adults as compared to older adults ($M_{\text{diff}} = 0.19$ versus $M_{\text{diff}} = 0.05$), which may have precluded this from constraining the specificity of subsequent retrieval-related reinstatement.

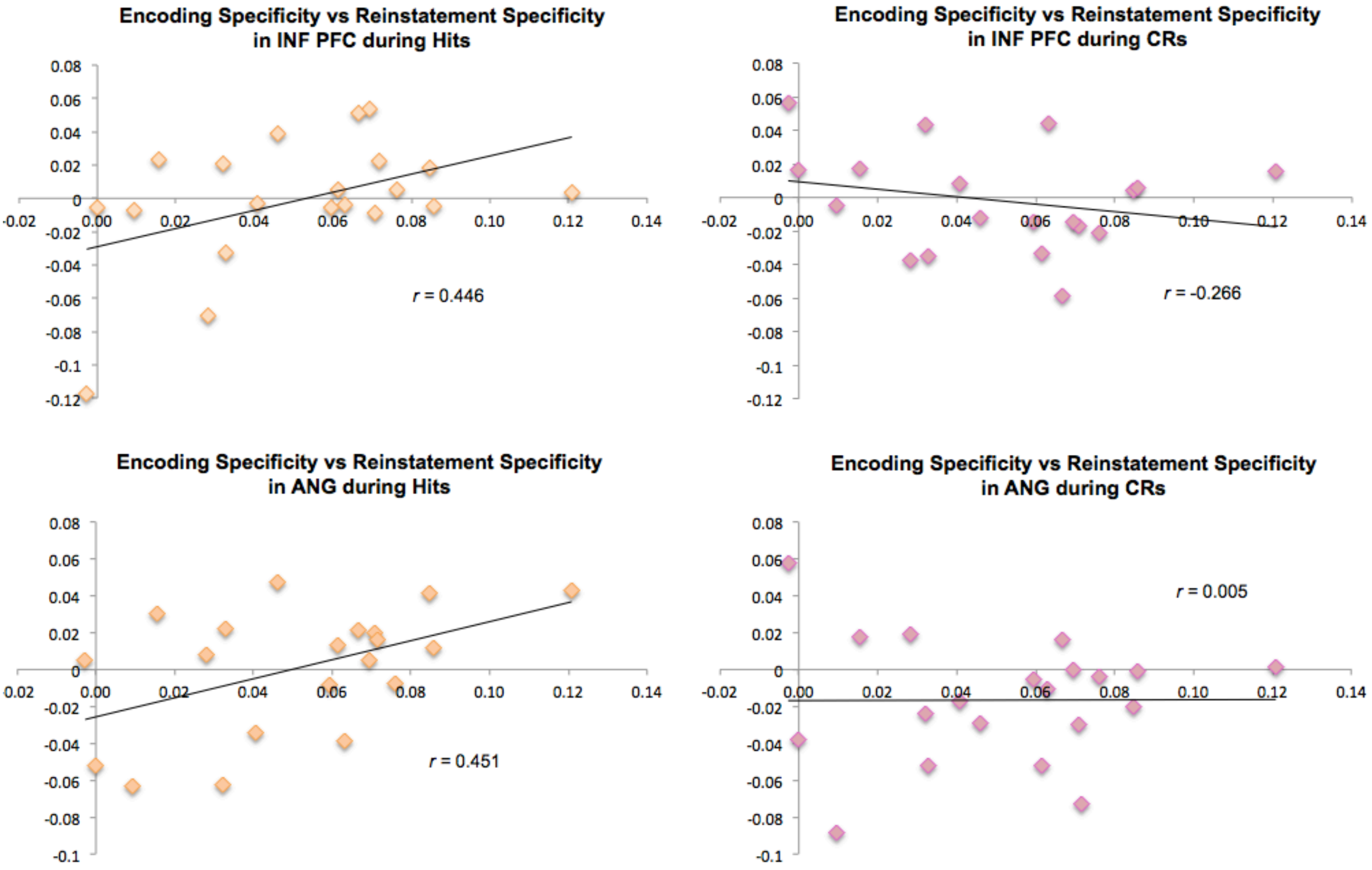

Figure 9. Category-level Reinstatement Specificity, calculated as Within-event ERS – between-event ERS (DC), during Hits (left) and Correct Rejections (right) in INF PFC (top) and ANG (bottom), plotted against encoding specificity in VVC, calculated as Same Category Similarity – Different Category Similarity. Only older adults data is shown. Higher encoding specificity is associated with greater reinstatement specificity during hits across both brain regions, but not during correct rejections.

Discussion

The present investigation sought to identify neural evidence for age-related changes in representational quality and strategic retrieval processes using pattern similarity analysis of fMRI data collected during an associative memory task. The results provide evidence for age-related changes in both these factors, with the observation of dedifferentiation of stimulus representations during encoding, as well as age-related declines in reinstatement of encoding-related activity during retrieval. In particular, activity patterns in ventral visual cortex exhibited reduced sensitivity to stimulus content during encoding in older adults as compared with younger adults. Moreover, whereas younger adults exhibited evidence for event-specific reinstatement of encoding-related activity (when comparing within-event versus between-event similarity for same exemplar trials) during both hits and correct rejections, older adults did not exhibit reinstatement effects. This was apparent even when reinstatement was assessed at the more lenient category-level (when comparing within-event versus between-event, different category trials), and despite the fact that, in some cases, older adults displayed higher levels of encoding-retrieval similarity overall. Instead, older adults exhibited the opposite patterns during correct rejections, with greater between-event ERS relative to within-event ERS. Although unpredicted, this pattern was associated with a lower incidence of false recognition among older adults, suggesting that it may have been advantageous to performance.

Age Differences in Representational Distinctiveness during Encoding

The observation of age-related declines in the distinctiveness of stimulus representations in ventral visual cortex during encoding is consistent with previous work identifying declines in the selectivity of neural responses in this region to different visual stimulus categories with age (Park et al., 2004; Carp et al., 2011; Johnson et al., 2015). In the present study, this pattern was driven by both reduced representational similarity between activity patterns of highly similar events, and increased similarity between activity patterns of dissimilar events, replicating previous work (Carp et al., 2011). This observation lends support to the proposal that aging is associated with declines in representational quality, at least for events comprised of visual stimuli. Future work will be necessary to assess whether this is also true for different types of event information (e.g., auditory, motor, tactile) that are supported by different areas of the brain areas, which may be affected by age to a greater or lesser degree. Unlike older adults, younger adults exhibited neural activity patterns that were highly sensitive to stimulus content, consistent with previous findings (e.g., Kriegeskorte et al., 2007; Kriegeskorte et al., 2008). Furthermore, younger adults who displayed greater neural distinctiveness during encoding also exhibited better memory performance, a relationship that has also been identified in previous work (Kuhl et al., 2012). This relationship is consistent with the idea that the quality of event representations impacts subsequent event memorability, at least when retrieval processes are intact, as in younger adults. One reason that the same relationship was less evident among older adults in the current experiment may be due to additional impairments operating at retrieval, which may have precluded a direct relationship between encoding quality and subsequent memory performance. Alternatively, reduced variability in encoding distinctiveness scores may have limited the ability to observe a correlation with subsequent memory among older adults.

Age Differences in Cortical Reinstatement during Correct Rejections

The present results identified robust evidence for event-specific reinstatement during successful associative recognition judgments among younger adults, but markedly less evidence for this phenomenon among older adults. Although this was true during both hits and correct rejections, this observation is particularly striking with respect to correct rejections to recombined pairs, wherein the test cue contains exemplar and category information that is incompatible with the original associate. Thus, reinstatement evidence, if observed, is unlikely to have simply been the product of retrieval cue processing, but rather likely reflects the retrieval of either specific or more general details of the original associate. This is in contrast to hits to intact pairs, wherein the test cue contains both exemplar and category information that is compatible with the original associate. As a result, reinstatement evidence, if observed, could plausibly arise due to retrieval of the original associate, or due to elaborative retrieval cue processing, such as visual imagery of the presented adjective-picture combination. This makes the source of reinstatement effects during hits, as observed in younger adults, more difficult to interpret than that during correct rejections. Thus, the pattern of results associated with correct rejections may provide the greatest insight into the retrieval strategies adopted by older and younger adults, which the current findings suggest may be qualitatively different.

In particular, during correct rejections to recombined pairs, younger adults exhibited evidence for event-specific reinstatement of encoding-related activity in both the angular gyrus and the inferior prefrontal cortex. That is, within-event ERS was greater than between-event ERS, even when the comparison event shared the same exemplar. The highly overlapping nature of the comparison condition suggests that this effect could not have been driven by retrieval of category, subcategory, or even exemplar information, but rather arose due to retrieval of specific details associated with the original word-picture pairing. This pattern suggests that younger adults engaged in goal-directed retrieval of the original word-picture association to make recognition decisions, consistent with the use of a ‘recall-to-reject’ strategy. These results complement previous behavioural and neuroimaging evidence from a number of different paradigms, including paired associate recognition (e.g., Cohn et al., 2008; Giovanello & Schacter, 2010), exclusion tasks (Jacoby et al., 1993; Gallo et al., 2010), and similar lure paradigms (e.g., Migo et al., 2009; Chapter 3; Bowman &

Dennis, 2016), which each suggest that younger adults engage this strategy to make recognition decisions. The present data lends further support to this idea, providing more direct neural evidence for the use of a recall-to-reject strategy by identifying reinstatement of event-specific encoding-related activity patterns during correct rejections of recombined pairs.

In contrast, evidence for event-specific reinstatement during correct rejections was not detected among older adults. Moreover, this was not accompanied by evidence for less specific, category-level reinstatement. This observation suggests that, at least in the current paradigm, older adults did not compensate for retrieval of highly specific details by retrieving more general, conceptual aspects of previous events to reject recombined pairs (e.g., recalling that *'Sparkling'* was paired with an object, but being unable to recall the particular associate). Interestingly, older adults did not simply fail to exhibit evidence for reinstatement during correct rejections, but instead exhibited the opposite pattern, whereby between-event ERS (DC) was greater than within-event ERS. That is, when presented with a recombined pair at test, such as 'Sparkling Office', having studied 'Sparkling Umbrella' previously, older adults exhibited a pattern of activity during retrieval that was more similar to that associated with the encoding of scene trials (e.g., trials involving the office) than to the corresponding encoding trial, during which the word 'Sparkling' was presented with an object (e.g., the umbrella).

Although this pattern was not expected, it may have been driven by perceptual or conceptual elaboration of the adjective-picture combination presented in the test cue, such as through visual imagery. In other words, when presented with the recombined pair 'Sparkling Office', older adults may have simply imagined or thought about a *sparkling office* to assess whether or not this concept or mental image felt familiar, rather than retrieve the image associated with *sparkling* in the study phase, as younger adults appear to have done. As the recombined pairs in the present experiment were always comprised of an associate from the opposite stimulus category, engaging in visual imagery of a recombined retrieval cue would be expected to produce activity patterns more consistent with the category presented in the cue, as compared that which the original associate belonged. This corresponds to the pattern exhibited by older adults, suggesting that this pattern may reflect a tendency for older adults to assess the familiarity of the retrieval cue, rather than attempt to retrieve the original associate. Interestingly, the degree to which older adults displayed this pattern was related to their ability to make correct rejections, which is consistent with the idea that older adults may have been able to use presence or absence of familiarity for the presented adjective-picture combination to support accurate recognition decisions. Although future work is necessary to ascertain whether this pattern is replicable, and whether it does indeed reflect the use of cue-related imagery during retrieval, this interpretation is nevertheless one possibility that is consistent with the current data.

The observation that older adults did not simply exhibit an absence of reinstatement effects, but rather a significant effect in the opposite direction, suggests that the failure to identify reinstatement effects in the older group did not arise due to insufficient power. Instead, the current results are consistent with the interpretation that reductions in evidence for cortical reinstatement during correct rejections among older adults reflects an age-related reduction in the ability to engage ‘disqualifying’ strategies, such as recall-to-reject, to correctly reject lures in a recognition test, as suggested by prior work (Jennings & Jacoby, 1993; Castel & Craik, 2003; Gallo et al., 2007; Cohn et al., 2008; Chapter 3). These findings complement previous work identifying age-related declines in reinstatement specificity during retrieval (St-Laurent et al., 2014; Johnson et al., 2015; Abdulrahman et al., 2016), and extend this work by providing evidence for age-related reductions in reinstatement of encoding-related activity during retrieval of trial-unique associations in a recombined recognition test. The observed declines in reinstatement may have arisen, at least in part, due to age-related declines in the ability to execute controlled and strategic retrieval processes, which are necessary to support to retrieval and evaluation of stored representations. Indeed, the present results are consistent with the possibility that older adults may have engaged alternative retrieval strategies that reduce demands on these processes, perhaps relying to a greater degree on cue familiarity to support recognition decisions, as suggested by previous behavioural and neuroimaging findings (Gallo et al., 2007; Cohn et al., 2008; Giovanello & Schacter, 2010; McDonough et al., 2013).

Age Differences in Cortical Reinstatement during Hits

If it is indeed the case that older adults were relying more on test cue familiarity to make recognition decisions, it is perhaps surprising that age differences in reinstatement were not mitigated during hits to intact trials, during which retrieval cues were congruent with the original associate (e.g., study ‘Wooden Umbrella’ and tested with ‘Wooden Umbrella’). These conditions were expected to reduce demands on controlled retrieval processes, and enable accurate responding, even on the basis of stimulus familiarity. As mentioned previously, during intact trials, even a retrieval strategy such as cue-related imagery (e.g., imagining a *wooden umbrella*) might be expected to yield reinstatement-like effects (e.g., greater within-event ERS relative to between-event ERS), as such imagery should generate activity patterns that are more similar to that which was present during the original encoding event (e.g., when

‘Wooden Umbrella’ was in view) as compared to an event from the opposite category (e.g., when a scene trial was in view). On the one hand, the absence of this pattern may indicate that older adults did not use the congruent retrieval cue to aid retrieval of stored details, nor did they engage in cue elaboration such as visual imagery during intact trials. That is, it may be the case that because these cues were congruent with a studied association, they elicited sufficient levels of familiarity to support a recognition decision in the absence of these additional cognitive operations.

Indeed, it may be the case that older adults only engaged in more extensive retrieval cue processing, such as visual imagery, in the absence of this initial familiarity. This possibility is consistent with the neural pattern similarity effects exhibited by older adults during correct rejections to recombined pairs.

An alternative, but not mutually exclusive, explanation comes from the observed relationship between neural distinctiveness during encoding and reinstatement specificity during hits to intact pairs. In particular, older adults who exhibited greater neural distinctiveness in ventral visual cortex during encoding also displayed greater reinstatement specificity during hits in the angular gyrus and inferior prefrontal cortex. This relationship suggests that the distinctiveness of neural activity patterns during perception of externally presented stimuli is related to, and may constrain, the potential specificity of neural activity patterns associated with internally generated images, such as those related to visual imagery or maintenance of retrieved content, as suggested by prior work (Kalkstein, Checksfield, Bollinger, & Gazzaley, 2011; Johnson et al., 2015). This observation raises the possibility that some older adults may have engaged in visual imagery of the retrieval cue, or even used the congruent cue presented on intact trials to successfully retrieve stored details, but that the associated neural activity did not meet the criteria for reinstatement evidence due to a decline in the specificity of neural representations with age. Importantly, this relationship was not observed during correct rejections, suggesting that age-related declines in representational quality during encoding are unlikely to fully account for age differences during retrieval. Instead, it may be the case that the ability to engage in further retrieval cue elaboration may have played a larger role in the emergence of cue-related imagery effects during correct rejections of recombined pairs, over and above individual differences in the specificity of neural representations.

Neural Basis of Cortical Reinstatement

When evidence for event-specific reinstatement of encoding-related activity was observed in the current study, these effects were localised in the angular gyrus and inferior prefrontal cortex. These results are consistent with previous work identifying event-specific reinstatement effects in the angular gyrus during cued recall (Kuhl & Chun, 2014; Bonnici et al., in press), as well as previous evidence for increases in regional BOLD activity in both inferior prefrontal and lateral parietal regions during strategic, recollection-based retrieval (Bowman & Dennis, 2016; Gallo et al., 2006; Gallo et al., 2010). The present results provide further insight into the contributions of these regions to successful recollection. In particular, the observation of reinstatement effects in the inferior prefrontal cortex suggests that this region not only guides strategic retrieval processes by selecting and monitoring content represented in different regions (Simons & Spiers, 2003), but also contributes to representing event-specific content, consistent with the role of this region in maintaining retrieved content in working memory (Dobbins, Foley, Schacter, & Wagner, 2002; Wagner, Maril, Bjork, & Schacter, 2004). Similarly, the observation of reinstatement effects in the angular gyrus during both hits and correct rejections lends support to existing proposals suggesting a role for the angular gyrus as an episodic 'output buffer' that maintains representations of retrieved content in the service of mnemonic decisions (Baddeley, 2000; Wagner et al., 2005; Vilberg & Rugg, 2008; Bonnici et al., in press). The observation that effects exhibited by older adults during correct rejections, which may be related to retrieval cue elaboration such as visual imagery, were also found in the angular gyrus suggests that the involvement of this region may not be selectively related to the maintenance of retrieved details from encoding, but perhaps supports any internal representations that are being used to inform mnemonic decisions.

In contrast to frontal and parietal cortex, event-specific reinstatement effects were not observed in the ventral visual cortex or the hippocampus in either age group, although evidence for category-level reinstatement was identified in ventral visual cortex during hits in younger adults. The latter observation is consistent with previous work identifying category, although not event-specific, reinstatement effects in ventral visual cortex (Kuhl & Chun, 2014). These findings are consistent with the sensitivity of this region to category information, as exhibited in the current study and in previous work (e.g., Carp et al., 2011; Kuhl et al., 2012). Similarly, previous studies have also failed to identify event-specific reinstatement effects in the hippocampus (Staresina et al., 2012; Kuhl & Chun, 2014). This may be due to insufficient image resolution to detect event-related activity patterns thought to be represented in specific hippocampal subfields, which may require higher resolution MRIs to be detected (e.g., Tompary et al., 2016).

Interestingly, the present study revealed little similarity between the pattern of results obtained from the univariate analysis of changes in regional BOLD activity and the multivariate analysis of distributed activity patterns within a given region, highlighting the complementary nature of these two analysis approaches (Davis et al., 2014). For example, despite the appearance of greater involvement of the angular gyrus during hits as compared to correct rejections based on univariate contrasts, this region was involved in maintaining event-specific activity patterns during correct rejections. This observation lends support to the idea that task-relevant information can be present in distributed activity patterns in a given region, even in the absence of overall increases in univariate signal strength. Similarly, despite the absence of age-related reductions in regional BOLD activity during encoding or retrieval, age differences in multiple measures of neural pattern similarity were identified. Although it is possible that age differences in univariate effects were not detected due to the specific contrasts used in the present study, and that group differences would have emerged if different conditions were compared (e.g., hits versus misses), this would not have altered the results of the multivariate analyses. This observation not only suggests that age differences in univariate signal strength cannot account for the reductions in neural pattern specificity observed during encoding or retrieval, but also highlights the value of combining these two analysis approaches when exploring group differences in brain-behaviour relationships.

Conclusions

Overall, the present results provide evidence for age-related changes in both representational quality and strategic retrieval processes as assessed through reinstatement of encoding-related activity at retrieval. In particular, older adults exhibited declines in neural distinctiveness during encoding, as well as an absence of evidence for event-specific or category-level reinstatement of encoding-related activity during retrieval, which was observed robustly in younger adults. Although some evidence was obtained to suggest that the distinctiveness of neural representations during encoding influences the potential specificity of representations during retrieval, this could not fully account for age differences in reinstatement during retrieval. In particular, evidence was also obtained which suggests that older and younger adults also engage qualitatively different strategies during retrieval. Whereas younger adults appear to recall details associated with the original associate to support recognition decisions, older adults were less likely to do so, and may have instead relied on a familiarity-based strategy that reduces demands on controlled and strategic retrieval processes. Taken together, the present data suggest that older adults may compensate for age-related declines in representational quality and attentional control processes by adopting retrieval strategies that minimise demands on these factors to support recognition memory performance.

Chapter 5

General Discussion

The experiments reported in this thesis were designed to explore the mechanisms underlying age-related decline in episodic memory. In particular, these experiments tested the hypothesis that age differences in memory for specific details of previous experiences could be explained through a combination of reductions in representational quality and impairments in controlled retrieval with age. To investigate this possibility, the contribution of these factors to memory performance was explored across three different experimental paradigms that each adopted a different operationalization of episodic memory. This not only enabled an assessment of the relative contribution of each of these factors to age differences in memory performance, but also tested whether the same account can be used to explain age-related memory impairment in the face of a great deal of methodological variability across studies. Across each of these experimental paradigms, converging evidence from behavioural, neuropsychological, and neuroimaging approaches was identified in support of the proposal that impairments in both representational quality and controlled retrieval processes contribute to age-related decline in episodic memory.

Summary of Findings

The results of Chapter 2 provided evidence that encoding strategies involving extensive, narrative elaboration that rely on prior knowledge lead to substantially greater enhancements in older adults' recall of concrete nouns, relative to strategies that involved meaningful, yet simple, binary judgments. This enhancement in recall performance suggests that these encoding strategies facilitated the creation of more distinctive and elaborative event representations, which aided subsequent retrieval in the absence of external cues. Nevertheless, older adults still recalled significantly fewer words than younger adults, suggesting a persistent decline in executing the controlled retrieval processes necessary for successful recall. Consistent with this idea, age differences in performance were reduced when memory was tested through recognition memory, but only for those items that were encoded using a highly elaborative strategy; age differences in recognition memory persisted for those items that were encoded using a simple binary strategy. The observation that combining elaborative encoding with the provision of strong retrieval cues was necessary to alleviate age differences in performance is consistent with contributions of both representational quality and controlled retrieval factors to age-related declines in free recall.

A similar pattern of results was obtained in Chapter 3 using a different paradigm that assessed recollection through the ability to discriminate between perceptually similar exemplars in an object recognition memory test. In particular, older adults exhibited increased false alarm rates to similar lures under test conditions that placed high demands on the use of controlled retrieval processes (e.g., Yes/No format), as well as under test conditions that enabled the use of more automatic, familiarity-based responding (e.g., Forced Choice format with corresponding foils). This pattern indicated that age differences could not be driven solely by impairments in controlled retrieval and evaluation of item details, and that age-related declines in the availability of unique object-level representations also reduced the ability to disambiguate targets and similar foils. This prediction was supported in a second experiment, in which the presence of interference from objects with overlapping features was manipulated, which is thought to modulate demands on representational complexity. Critically, reducing the amount of perceptual interference faced by older adults lessened age differences in performance in the Forced Choice test, providing evidence for age-related declines in representational quality that leads to greater vulnerability of older adults to the effects of interference. In contrast, age differences in Yes/No performance were still observed, consistent with an age-related impairment in the ability to engage strategic recall-to-reject processes, even under conditions of reduced interference. Together, these results are consistent with age-related decline in both representational quality and controlled retrieval processes providing an explanation for impaired object recognition memory with age.

The neuropsychological test data presented in Chapter 3 lent additional support to this proposal by identifying relationships between multiple cognitive measures and mnemonic discrimination ability among older adults. In particular, a relationship was observed between a measure of representational quality derived from a perceptual task and Forced Choice memory performance, as well as the size of the benefit older adults could gain from the provision of retrieval support, consistent with a critical role for complex object representations to support accurate simultaneous discriminations. A relationship was also identified between executive function and recall ability and recognition memory performance across both test formats. This result highlights the role of these factors in the ability to make mnemonic discriminations between similar lures, likely through supporting the execution of a recall-to-reject strategy, which is highly beneficial to performance. As these neuropsychological tests are thought to reflect the function of medial temporal and prefrontal regions, these results suggest that individual variability in brain structure or function may be contributing to heterogeneity in performance across older adults.

The results of Chapter 5 provide support for this idea by identifying age differences in the information contained in neural activity patterns during encoding and retrieval of associative memories using multivariate fMRI. In particular, this experiment revealed dedifferentiation of activity patterns in ventral visual cortex during encoding of word-picture pairs, characterised by reduced pattern similarity between events with similar stimulus content, coupled with increased pattern similarity between events containing dissimilar content, replicating previous work. The results also provided evidence for age-related declines in the use of strategic retrieval processes at test; whereas younger adults exhibited event-specific reinstatement of encoding related activity during hits and correct rejections, suggesting the use of a recall-to-accept/reject strategy, older adults did not display evidence for such reinstatement, nor for more general reinstatement of category level information. Although age differences in reinstatement specificity during hits appear to arise, at least in part, due to declines in representational distinctiveness during encoding, this was not the case during correct rejections, suggesting that age differences in retrieval strategies also contribute. In particular, older adults may have compensated for declines in attentional control processes and representational quality by adopting a more automatic, familiarity-based strategy to make recognition decisions. Taken together, these results provide evidence for dedifferentiation of stimulus representations with age, as well as an age-related reduction in the engagement of controlled and strategic retrieval strategies.

Overall, the results of the series of experiments presented in this thesis provide converging evidence from three different experimental paradigms in favour of the contribution of multiple factors to age-related decline in episodic memory, including reductions in the quality of event representations, and impairments in controlled retrieval of event details. These experiments differed substantially with respect to a number of methodological variables, including in the stimuli used, the way in which stimuli were encoded, the format in with which memory was tested, and the features of prior experience that were the target of memory retrieval. In spite of these large variations in methodology, as well as individual differences likely present across the different groups of older adults being tested in each experiment, the results across chapters nevertheless point to the same conclusions. The consistent pattern observed across experimental paradigms provides evidence that this outcome is not driven by a specific set of stimuli or task instructions, but rather the consequence of common demands shared across experiments, namely the need to recover specific, rather than general details, from memory through the use of controlled and deliberate retrieval processes. Accordingly, these results suggest that a common set of explanatory variables may be sufficient to account for age differences in memory for specific details of past experiences, irrespective of how episodic memory is operationalized in a given experiment.

Generalisability of the Present Findings

The current set of experiments examined only three different experimental paradigms, however it is predicted that representational quality and controlled retrieval can explain the presence or absence of age differences in memory performance across a variety of different test conditions. To demonstrate this point, it is important to consider both the nature of the representation required to perform a particular task, as well as the control processes that must operate on these representations to perform the task effectively. As described throughout this thesis, age differences in performance on a given task are predicted to be determined by two conditions: i) the degree to which a task necessitates, complex, rather than simple, representations, and ii) the degree to which the task demands controlled, rather than automatic, processes. When demands on one or both of these factors are present, age-related impairments in performance are predicted to emerge. Conversely, when demands on both of these factors are minimised, age differences in performance should be attenuated. This idea gained support through the results presented in Chapters 2 and 3, and is also predicted to explain the presence or absence of age differences in a number of task contexts.

For example, take the widely held view that older adults exhibit declines in recollection, coupled with relatively preserved familiarity. This interpretation of older adults' memory performance is based on the assumption that familiarity is an automatic process, whereas recollection is a controlled process, an idea that has received a great deal of support (Jacoby, 1991; Yonelinas, 2002). However, the automatic/controlled distinction is not the only respect with which these two measures typically differ. In particular, the tests that are used to assess recollection as compared to familiarity also typically require a more complex event representation. For example, familiarity estimates often assess memory for the gist of an item (e.g., was an *umbrella* presented?) and therefore only require a very simple representation, whereas recollection typically assesses memory for a more complex conjunction of item and contextual features (e.g., was *umbrella* presented in context A?). Thus, these test conditions differ on not one, but two or potentially more dimensions (see also Cowell et al., 2010).

In the present view, examples of disproportionate deficits in recollection-based measures as compared to familiarity arise not only due to differences in demands on controlled processes between these conditions, but also due to differences in demands on representational quality. For example, in an inclusion/exclusion task, accurate performance on the inclusion condition relies on increased fluency (e.g. familiarity) for a single item, thus reducing demands on both factors. In contrast, exclusion conditions require both controlled processes (e.g., recall to reject) as well as a representation of the conjunction of the item and the context in which it was originally presented. Similarly, in an associative recognition task, hit rates to intact pairs can be accomplished via increased fluency and a representation of individual items, whereas rejecting rearranged pairs necessitates a representation of a specific conjunction of items, coupled with the use of controlled retrieval processes to access that representation. Finally, in a Remember/Know paradigm, ‘know’ responses can be made on the basis of a simple item representation, whereas ‘remember’ responses entail a more complex representation of the encoding event, such as details about the spatiotemporal context in which the item was encountered. Thus, across tests that are typically used to measure age differences in recollection and familiarity, performance is also critically determined by the availability of complex as compared to simple event representations.

Accordingly, to properly assess whether ‘familiarity’ (e.g., more automatic, rather than controlled retrieval) is intact with age, performance must be measured under conditions that nevertheless still require a complex representation to make a successful judgment. Under these conditions, the present account predicts that age differences would be likely to emerge. The experiments in Chapter 3 provide one example of support for this prediction by demonstrating age-related impairments in forced choice recognition of objects with similar foils. Although performance in a Forced Choice test with corresponding foils can be supported by familiarity (Holdstock et al., 2002; Migo et al., 2009), accurate familiarity-based decisions in this task necessitate the processing of complex representations due to the feature overlap between targets and foils. The observation that older adults were impaired under these conditions indicates that familiarity is not intact with age when the test requires complex stimulus representations.

Another example in the literature comes from age-related impairments in recognition memory for unfamiliar faces (Crook & Larrabee, 1992; Searcy, Bartlett, & Menon, 1999). Critically, the same pattern of deficits is observed as that for object recognition memory with similar foils, namely an increase in false recognition of novel faces with age, coupled with an intact hit rate towards studied faces (Bartlett, Strater, & Fulton, 1991; Searcy et al., 1999). This pattern holds even under conditions of forced choice recognition (Boutet & Faubert, 2006), where a reliance on familiarity should be sufficient to support accurate responding (Migo et al., 2009; 2014). Importantly, faces represent an example of naturally occurring stimuli that share a high degree of feature overlap, and therefore require a more complex, conjunctive representation to support accurate discrimination. Indeed, evidence from neuroimaging and patient work has identified a role for the perirhinal cortex in supporting these representations (Lee, Levi, Davies, Hodges, & Graham, 2007; O'Neil, Cate, & Kohler, 2009; Barense et al., 2010), the same region that is thought to support conjunctive representations of complex objects (Cowell et al., 2006). Thus, age-related impairments in face recognition, even under conditions where familiarity should be sufficient to support performance, are consistent with a decline in representational quality with age due to dysfunction of the perirhinal cortex (see also Burke et al., 2012). Such examples argue against the idea that age-related memory deficits can be explained by intact familiarity coupled with impaired recollection. Instead, they suggest that measurements of familiarity typically do not detect age differences because they create conditions whereby simple, rather than complex, representations are sufficient to support performance.

Of course, one might argue that age differences that emerge under conditions that are thought to be supported by more automatic, familiarity-based responding, arise not because of age differences in representational quality, but instead because younger adults are more likely to spontaneously engage strategic retrieval processes that result in significant gains in memory performance. Indeed, the fact that representational quality is often inferred by one’s ability to retrieve a given memory trace is an important limitation of the studies described above, including those presented in Chapters 2 and 3. This issue makes it difficult to discern whether age differences in representational quality are driving performance impairments, even when efforts have been made to reduce demands on controlled retrieval. Exploring the effects of task manipulations that are predicted to impact representational demands, but keep demands on controlled retrieval constant, as undertaken in Chapter 3, is one way to try to control for these effects. Another way of assessing this behaviourally is by adopting implicit measures of memory that are not accessible to conscious awareness, thus eliminating the possibility that age differences in performance arise due to reductions in controlled processes. According to the current proposal, that aging is associated with declines in both representational quality and controlled retrieval, the presence of age differences in a task that minimizes demands on controlled processes is predicted to be determined by the degree to which it places demands on a high degree of representational complexity.

Notably, implicit memory is often preserved in older adults, a finding which has contributed to the present understanding that aging affects controlled processes but leaves automatic processes relatively intact. However, much of this evidence comes from paradigms that also place minimal demands on representational complexity, such as age-invariant priming effects (e.g., response facilitation) to trial unique stimuli under conditions of low interference. These studies therefore minimize demands on both factors, such that intact performance is consistent with the present proposal. However, recent experiments using eye tracking to measure non-conscious exploration (e.g., fixations) of visual stimuli during passive viewing suggest that the absence of age differences in implicit tests of memory depends on the level of interference present in the paradigm. These tests take advantage of the novelty preference, or the tendency to make a greater number of fixations to novel as compared to previously viewed stimuli. A reduced preference for novel stimuli is thought to reflect implicit false recognition, whereas a novelty preference for studied stimuli would suggest forgetting. Studies using this method have identified evidence for age-related reductions in the novelty preference, selectively under conditions that place increased demands on representational complexity.

For example, in a study that involved passive viewing of repeated scenes with overlaid objects in identical or altered configurations (Ryan et al., 2007), younger adults made more fixations towards the altered object-location relations within the scenes, whereas older adults did not. This reduced novelty preference suggests that older adults did not possess a representation of sufficient quality containing the relationship between objects and the scene, consistent with age-related declines in hippocampal function, a region which is thought to support representations at that level of complexity (Cowell et al., 2009). A similar result was observed in a study involving passive viewing of everyday objects that shared either a high or low degree of feature overlap. Older adults exhibited a reduced novelty preference for objects that shared overlapping features with previously viewed objects, but not for objects that did not share overlapping features (Yeung et al., 2013). Thus, older adults treated similar objects as though they were familiar, consistent with declines in the availability of complex object representations supported by perirhinal cortex (Burke et al., 2012), but could perform normally when demands on these representations were reduced, and more simple feature level representations were sufficient to support novelty processing (Cowell et al., 2006).

These findings highlight the possibility that feature overlap between targets and foils, as well as the type of stimulus (e.g., scenes, objects) contributes to the level of representational complexity required to discriminate between stimuli, and determines which brain areas will be critical for supporting these representations, and therefore task performance (Cowell et al., 2010). However, another important factor that can drive the representational demands of a given task is the degree of interference from intervening items that also share common lower level features. As demonstrated in Chapter 3, as well as in prior work (Cowell et al., 2006; Eacott et al., 1994), manipulating the number of such items can dramatically impact performance (e.g., 60 objects vs 180 objects studied), and the presence or absence of age-related impairments. Despite growing evidence in the literature that increased interference has a greater impact on older adults relative to younger adults, interference is a factor that is rarely emphasised or held constant across different investigations. Accordingly, this factor, when not explicitly controlled, can give rise to apparently contradictory evidence from different paradigms that are thought to measure the same processes, but possess different levels of interference.

An example of this comes from an object recognition memory study with similar lures that observed age-related impairments in explicit memory, coupled with intact implicit memory for specific details, evidenced by intact priming effects (e.g., facilitated responding for identical repeats but not similar lures) (Koutstaal, 2003). These results were interpreted as evidence that age differences in the ability to discriminate between similar lures are driven by impaired retrieval processes alone. However, it is also possible that the demands on representational quality in this particular experiment did not exceed that which was available to older adults. Critically, this pattern of intact performance was observed under conditions in which interference from intervening items was already quite low (e.g., only 30 objects studied). Thus, it may be the case that these relatively low levels of interference were insufficient to impair implicit memory in older adults. Although this possibility remains to be tested, such an outcome would be consistent with numerous examples of interference-dependent impairments in memory and perception with age (Burke et al., 2010; 2011; Newsome et al., 2012; Ryan et al., 2012; Yeung et al., 2013). This possibility highlights the importance of considering not only demands on controlled versus automatic processes when exploring age-related changes in memory performance, but also the representational demands inherent to the task.

Contributions to Existing Theories of Cognitive Ageing

The present proposal shares overlapping elements with several previous theories of episodic memory decline in healthy ageing, and makes many similar predictions. However, the primary way in which it offers an advance is in providing a unifying framework that may help to resolve some of the disagreements between previous theories, as well as account for apparently contradicting findings in the literature. Some of these instances were described above, such as the presence versus absence of age differences in implicit measures of memory and in measures of familiarity-based responding in recognition memory. These apparent contradictions may be accounted for by combining existing ideas about disproportionate age-related impairment in controlled, as compared to automatic, forms of memory retrieval (e.g., Craik & Byrd, 1982; Hasher & Zacks, 1979; Jennings & Jacoby, 1993), with age-related decline in representational quality (Ryan et al., 2012; Burke et al., 2014). That is, if one considers the amount of interference in a given task, together with increased vulnerability to interference with age as the result of reduced availability of conjunctive representations that can resolve ambiguity between overlapping inputs, impairments in more automatic forms of memory retrieval are no longer counter to predictions.

Similarly, the present proposal may be able to resolve the contradicting views of the *Associative Deficit Hypothesis,* which states that older adults cannot form new associations, and the *Hyper-binding Hypothesis*, which states that older adults form too many associations due to declines in inhibitory control, by combining aspects of both of these ideas. In particular, the current hypothesis states that age-related declines in representational quality reduce the availability of complex representations of feature conjunctions and item-item/context conjunctions that are supported by the medial temporal lobe, consistent with the Attention Deficit Hypothesis. This leaves older adults more vulnerable to interference from irrelevant or previously relevant information that share common elements (e.g., spatially or temporally contiguous items and features), which older adults may be less able to inhibit due to declines in cognitive control processes, as described by the Hyper-Binding Hypothesis, thus compounding the deficit. Moreover, declines in controlled processing during retrieval together with reduced availability of unique stimulus representations would leave older adults less able to overcome the sense of familiarity elicited by stimuli that overlap not only with studied targets but also distractors, leading to characteristic patterns of false recognition.

Finally, the present proposal may also be able to reconcile views that age-related declines in mnemonic discrimination of objects with overlapping features arises due to declines in pattern separation ability due to hippocampal dysfunction (Stark et al., 2010), versus declines in the availability of complex object-level representations due to perirhinal dysfunction (Burke et al., 2012). In particular, data from the present experiments suggest that perhaps by considering the role of controlled retrieval, namely recall to reject processes, apparently contradictory data can be accommodated. In particular, there is much evidence that mnemonic discrimination deficits in Forced Choice test formats can be linked to the perirhinal cortex, whereas the hippocampus appears to be essential for Yes/No recognition (Holdstock et al., 2002; Westerberg et al., 2006; 2013). Similarly, the results of Chapter 3 provided evidence consistent with the idea that representations supported by perirhinal cortex only determine performance when demands on controlled retrieval were reduced (e.g. Forced Choice). One reason for differences between test formats may be the requirement for recall to reject in Yes/No recognition, but not in Forced Choice recognition. Importantly, recall-to-reject processes are thought to rely on hippocampal-mediated computations, such as pattern completion (Bowman & Dennis, 2016). From a representational hierarchical perspective, recall-to-reject processes may be understood as relying on not just a representation of the object, but also a representation of the object in temporal context (e.g. the first presentation). A representation at that level of complexity would be unlikely to be supported by the perirhinal cortex, but rather by the hippocampus (Cowell et al., 2010), consistent with the critical role of this region in Yes/No recognition.

Thus, an examination of some of the existing hypotheses of cognitive ageing suggests that emphasising *either* age-related declines in representational quality or controlled processes alone, often leads to apparent contradictions between views. However, the current proposal suggests that these discrepancies can often be explained by taking the second factor into greater consideration, by considering how the two factors may interact, and how these interactions might vary according to different task conditions (e.g., test format, stimulus type, etc.). Importantly, the proposal that ageing is associated with declines in both representational quality and controlled processes not only helps to resolve some inconsistencies within the memory literature, but also helps to explain a broader set of cognitive deficits exhibited by older adults outside of the domain of memory. In particular, the present proposal predicts that older adults should exhibited impaired performance on any task that places demands on complex representations supported by the medial temporal lobes, and controlled processes supported by the prefrontal cortex.

Representational Quality & Cognitive Control Beyond the Memory Domain

Evidence in support of this prediction comes from observations that age-related impairments are often not limited to tests of episodic memory, but can also extend to other domains such as perception, future thinking, and navigation. For example, previous work has identified age-related impairments in perceptual discrimination of complex objects when targets and foils share overlapping features, but not when they are more distinct (Burke et al., 2011; Ryan et al., 2012). This pattern has also been accompanied by reduced activity in the perirhinal cortex in older adults (Ryan et al., 2012) and altered firing rates in perirhinal neurons in aged rodents (Burke et al., 2014), lending support to the proposal that impaired performance on these tasks arises due to declines in the availability of object-level representations supported by this region (Burke, Ryan, & Barnes, 2012). Similarly, older adults are also impaired in perceptual discrimination of unfamiliar faces, such that they require greater dissimilarity between faces before they can discriminate them successfully (Goh et al., 2010; Lee, Smith, Grady, Hoang, & Moscovitch, 2014), consistent with a decline in the availability of conjunctive representations necessary to disambiguate similar faces, which are thought to be supported by perirhinal cortex (O'Neil et al., 2009; Barense et al., 2010).

Older adults have also been shown to exhibit impairments in the ability to imagine future events, typically producing narratives that lack vividness and episodic richness, and which contain fewer internal details (e.g., specific perceptual and spatiotemporal features) and a greater number of external details (e.g., general semantics; Addis, Wong, & Schacter, 2008; Gaesser, Sacchetti, Addis, & Schacter, 2010). Notably, this is the same pattern that is often exhibited by older adults during the retrieval of autobiographical memories from the past (Levine et al., 2002). This similarity in performance across tasks is consistent with numerous observations that imagining future events recruits a similar network of brain areas as autobiographical memory retrieval, including medial and lateral temporal lobes, prefrontal, and parietal regions (Addis, Wong, & Schacter, 2007). This overlap in neural recruitment may reflect the shared cognitive control processes and representational demands necessary to support event construction and elaboration across both tasks, including retrieval of semantic and perceptual details from memory, and combining and maintaining these elements within a spatiotemporal context in an online event representation (Addis et al., 2007; Hassabis & Maguire, 2007). Consistent with age-related declines in these processes, previous work has identified age-related reductions in the recruitment of prefrontal, medial temporal and parietal regions during construction and elaboration of future events (Addis, Roberts, & Schacter, 2011).

Finally, older adults can also exhibit deficits in route learning and spatial navigation of novel environments (Moffat, Zonderman, & Resnick, 2001; Moffat & Resnick, 2002). Such impairments are consistent with age-related decline in the ability to form configural representations of the spatial relationships between landmarks in the environment, which are supported by the hippocampus (Iaria, Palermo, Committeri, & Barton, 2009). The impaired use of allocentric, or place-learning, navigation strategies described above is also thought to arise due to the demands they place on executive and strategic function, leading to the selection of inefficient spatial search strategies, impaired behavioural monitoring, and perseveration of ineffective search behaviour (Moffat & Resnick, 2002). Indeed, older adults' performance in virtual navigation tasks has been positively associated with prefrontal gray matter volume and white matter integrity (Moffat, Kennedy, Rodrigue, & Raz, 2007). Consistent with declines in the ability to meet the representational and strategic demands associated with allocentric spatial navigation, older adults are more likely to rely on egocentric, or response learning, strategies that are supported by the striatum and can be acquired through automatic, procedural learning (Rodgers, Sindone, & Moffat, 2012; Schuck, Doeller, Polk, Lindenberger, & Li, 2015). Similarly, previous work has not found age differences in navigation performance to be significantly reduced for well-learned routes (Rosenbaum, Winocur, Binns, & Moscovitch, 2012), which do not rely on online representations supported by the hippocampus (Maguire, Nannery, & Spiers, 2006), but instead are thought to be supported by schematic cortical representations that remain intact with age.

Taken together, evidence from behavioural and neuroimaging research has identified age-related impairments in perception, future thinking, and navigation that are consistent with a combination of declines in representational quality and cognitive control processes. These findings complement those from studies of episodic memory, lending further support to the proposal that aging is associated with significant declines in both of these factors, which not only impacts memory function, but also performance in other tasks that incur similar demands. This evidence from other domains also helps to provide further insight into the neural mechanisms underlying age-related declines in cognitive control processes and representational quality by identifying common brain regions that are associated with age differences in performance across tasks.

Neural Basis of Declines in Representational Quality and Controlled Retrieval

As discussed throughout this thesis, a great deal of evidence from previous research has linked age-related impairments in episodic memory with declines in the function of the prefrontal cortex and the hippocampus. The results of the present experiments provide further evidence for this idea, identifying a relationship between older adults' performance on neuropsychological tests measuring frontal and hippocampal function, and mnemonic discrimination performance in Chapter 3, as well as evidence for age-related reductions in cortical reinstatement in prefrontal cortex in Chapter 4. Existing work has also observed age-related changes in the recruitment of posterior sensory regions during encoding and retrieval, as well as alterations in the sensitivity of these regions to different stimulus input. The results of Chapter 4 are consistent with these observations, providing evidence for declines in representational specificity in ventral visual cortex during encoding, as well as a relationship between representational specificity at encoding and reinstatement specificity during retrieval. Similarly, the results of Chapter 3 provide evidence for a relationship between a perceptual measure of representational quality that is sensitive to perirhinal cortex function, and subsequent recognition memory performance in older adults, lending further support to recent proposals that aging is associated with alterations in the function of this region. Taken together, the present findings complement existing research, and emphasise the idea that the age-related changes brain function that contribute to memory decline also have implications for age differences in other aspects of cognition.

The present results also add to a growing body of work suggesting that age differences in the contributions of frontal, medial temporal, and ventral visual cortical regions to task performance may not always manifest as simple increases or decreases in regional BOLD activity, but can also arise through differences in the information carried in distributed neural activity patterns. For example, in the experiment presented in Chapter 4, evidence for age-related reductions in the specificity of neural activity patterns during encoding and retrieval were identified in the ventral visual cortex, prefrontal cortex, and angular gyrus, despite the absence of significant age differences in regional BOLD activity in any of these regions. These results complement previous work that has identified reduced differentiation of neural activity patterns among older adults during perception (Carp et al., 2010; Johnson et al., 2015), working memory (Payer et al., 2006; Carp, Gmeindl, & Reuter-Lorenz, 2010) and long-term memory retrieval (St-Laurent et al., 2014; Abdulrahman et al., 2016), and highlight the utility of multivariate analysis approaches to characterising the mechanisms underlying age-related declines in performance in a variety of tasks. Indeed, a consistent pattern that has emerged across experiments is a tendency for older adults to exhibit neural activity patterns characterised by reduced responsivity to task demands and reduced selectivity to different inputs, resulting in less distinctive neural representations across conditions.

Although the current experiments cannot provide further insight into the neurobiological changes underlying age-related reductions in neural distinctiveness, existing evidence suggests that one possible cause may be deficient neuromodulation, arising due to age-related changes in neurotransmission (Li, Lindenberger, &

Sikstrom, 2001). To date, two neurotransmitter systems have been identified that may be particularly relevant to age-related decline in cognitive control processes and representational quality, including dopamine (DA) and γ-aminobutyric acid (GABA). For example, reductions in dopaminergic modulation have been linked to older adults' performance in measures of executive function, working memory, and episodic memory (Volkow et al., 1998; Bäckman et al., 2000; see Bäckman, Nyberg, Lindenberger, & Farde, 2006 for review). Furthermore, dopamine has been shown to influence measures of regional BOLD activity (Morcom et al., 2010; Backman et al., 2011) and neural specificity (Abdulrahman et al., 2016) in the prefrontal cortex and the hippocampus, suggesting a possible role for this neurotransmitter in age-related changes in neural recruitment and differentiation.

Similarly, declines in GABA-mediated intracortical inhibition have been linked to age-related reductions in the selectivity of neural responses in early and late visual cortical regions (Leventhal, Wang, Pu, Zhou, & Ma, 2003). In particular, single neuron recording in aged monkey shave identified evidence for increased responding to non-preferred orientations and directions, as well as increases in spontaneous and irregular firing rates (Schmolesky et al. 2000; Leventhal, et al., 2003; Liang et al., 2010). These changes are thought to underlie declines in visual function with age (Spear, 1993), and may contribute to observed differences in the selectivity of visual cortical regions in fMRI studies of aging, as well as age differences in performance in perceptual and mnemonic tasks that rely on the integrity of these representations. Taken together, these observations raise the possibility that alterations in neurotransmitter systems may contribute to some of the age differences in neural recruitment and differentiation identified across neuroimaging studies, and represent a possible mechanism underlying age-related declines in cognitive control processes and representational quality.

Future Directions

The present experiments provide evidence to suggest that age-related decline in both representational quality and controlled retrieval processes contribute to age differences in episodic memory. However, it is important to note that there was also a substantial amount of individual variability in behavioural performance and neural measures among older adults across experiments. This variability was highlighted in the results presented in Chapter 3, wherein older adults who scored higher in measures of executive function, recall ability, and representational quality performed significantly better than low scoring older adults in mnemonic discrimination of targets and similar foils. Such observations are not unique to the current investigation; substantial differences in memory performance between older adults scoring high and low in similar neuropsychological tests have been identified in a number of previous studies (Glisky, Rubin, & Davidson, 2001; Davidson & Glisky, 2002; Holden et al., 2013; Stark et al., 2013 Reagh et al., 2014; Reagh et al., 2016), with high scoring older adults often outperforming their lower scoring counterparts on various behavioural measures of episodic memory, and sometimes performing as well as younger adults.

These observations highlight the heterogeneity inherent in cognitive ageing, with some older adults experiencing more dramatic declines in episodic memory than others. Although such findings are apparent in cross-sectional studies, this point can be best demonstrated through longitudinal studies that follow neural and behavioural changes in the same individuals for decades (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012). In particular, previous studies have found that although the majority of individuals exhibit a pattern of decline typical for their age group, other individuals maintain high and stable memory performance throughout the lifespan, whereas others exhibit a more dramatic rate of decline than others in their age group (Josefsson, Luna, Pudas, Nilsson, & Nyberg, 2012). This variability may result from individual differences in the rate of decline in brain structure and function (Persson et al., 2011), which is thought to be determined by a combination of genetic predisposition and lifestyle factors, such as education, occupation, and physical activity (Josefsson et al., 2012; Nyberg et al., 2012).

Thus, an important limitation of the present research, which is inherent to cross-sectional studies of cognitive ageing, is that age-related memory deficits may be over-estimated or under-estimated, depending on the particular make-up of a given elderly sample. Furthermore, cross-sectional studies may be subject to cohort effects, or generational differences between younger and older adults in factors such as educational attainment, which may inflate age differences in memory performance (Nyberg et al., 2012). Thus, although the results of the present studies and those reviewed in the literature are consistent with the proposal that age-related episodic memory impairment arises due to declines in representational quality and controlled retrieval processes, this may not accurately characterise all older adults, or at least not to the same degree. Converging evidence from future work using longitudinal designs or larger population-based samples, which can better capture this individual variability, are essential for assessing the degree to which these two factors still do well in explaining age-related decline in episodic memory once this variability has been accounted for.

The observed heterogeneity within the ageing population is not simply a challenge for characterising the neural and behavioural changes that are typical of healthy ageing, but also raises the important question as to whether some of the observed changes do not reflect healthy ageing, but instead are indicative of underlying neural pathology that is associated with preclinical mild cognitive impairment (MCI) or Alzheimer's Disease (AD). Although all of the participants included in the current studies performed within the normal range on the Montreal Cognitive Assessment (MoCA), a dementia screening test thought to be sensitive to MCI, it is nevertheless possible that some of these individuals were harbouring neural changes associated with preclinical AD. In particular, previous work has identified β-amyloid deposition and tau pathology in the medial temporal lobes, particularly in the entorhinal (ERC) and perirhinal (PRC) cortex, of healthy older adults that do not have a diagnosis of MCI or AD (Jagust, 2013; Schöll et al., 2016). This raises the possibility that certain age-related declines in performance, particularly those that have been associated with declines in entorhinal and perirhinal cortical function, may be a sign of early AD pathology and possible progression to MCI or AD.

Indeed, previous work has found that community-dwelling older adults that have been identified as at-risk for MCI due to performance below the normal range on the MoCA, exhibit increased vulnerability to interference in measures of both memory and perception (Newsome et al., 2012; Yeung et al., 2013) that are thought to be sensitive to underlying ERC/PRC pathology (McTighe et al., 2010; Barense et al., 2012). However, the results presented in Chapter 3 identified analogous patterns of behavioural performance among older adults who performed within the normal range on the MoCA, but who performed more poorly in different measures, such as representational quality and recall ability, a pattern which has also been observed elsewhere (Holden et al., 2013; Stark et al., 2013; Reagh et al., 2014; 2016). Such observations raise the possibility that certain experimental paradigms, particularly those that have been identified as sensitive to ERC/PRC function, may be better suited to early detection of AD pathology among older adults than existing cognitive screening tests. Given the expense associated with PET imaging that is necessary to measure β-amyloid deposition and tau pathology in vivo, exploring the utility of inexpensive behavioural measures for identifying older adults who may be at-risk for developing MCI and AD is an important direction for future research.

Conclusions

Together, the experiments presented in this thesis lend support to the proposal that episodic memory decline in healthy ageing arises due to a combination of reductions in representational quality and impairments in controlled retrieval processes. This hypothesis was supported by converging evidence from behavioural, neuropsychological, and neuroimaging evidence from three different experimental paradigms that each adopted a different operationalization of episodic memory, but nevertheless shared in common demands on controlled and deliberate retrieval of specific details of previous episodes. The consistency of these results across different methodologies raises the possibility that these factors may not only help to explain age differences in episodic memory, but also other aspects of cognitive decline affecting the elderly population.

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